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Causes and Consequences of Altered Avian Communities in Response to Anthropogenic Noise

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CAUSES AND CONSEQUENCES OF ALTERED AVIAN COMMUNITIES IN RESPONSE TO ANTHROPOGENIC NOISE

by

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Causes and consequences of altered avian communities in response to anthropogenic noise

Dissertation directed by Professor Alexander Cruz

Human-generated noise pollution has emerged swiftly on a global scale and it presents an evolutionarily novel condition for species that rely on acoustic communication, especially birds. Noise may mask or interfere with bird communication, limiting bird distributions or resulting in lowered reproductive success. However, studies have not definitively linked bird declines to noise because other mechanisms could explain declines, such as confounding noise exposure with edge habitat, vehicular motion and lights, and mortality from bird-vehicle collisions.

My study design provided a “natural experiment” that eliminated the influence of confounding factors common to noisy habitats and isolated noise as a single experimental variable to determine whether noise negatively influences birds via acoustic masking and to explore the consequences of noise exposure on ecological communities. I found that noise reduces nesting species richness and alters community composition. Species-specific tolerances to noise appear to be explained by vocalization frequency: species that avoid noisy habitat have low frequency vocalizations, and are larger bodied, and those tolerant of noise are smaller and have higher pitched vocalizations that escape acoustic masking by low-frequency noise. Despite this general trend, some, but not all, species adjust vocal signals in response to

noise, which may permit them to be heard in noisy habitats. In terms of nesting success, and contrary to expectations, birds nesting in noisy areas benefit from increased reproductive success due to less nest predation. This pattern was observed for real nests and confirmed with artificial nest experiments. Finally, through landscape-level modeling efforts, I demonstrate that noise can be effectively managed to minimize the influence of this novel disturbance on natural communities.

These findings have broad implications for noisy habitats around the world: (i) if higher nest success is widespread in noisy environments, it may help explain the general success of many synanthropic species and the homogenization of urban avian communities, (ii) acoustics can structure avian communities, though nonrandomly, (iii) noise may have unexpected indirect effects on ecological communities due to species-specific responses to noise by species with important ecological roles, but (iv) mitigation efforts can successfully reduce the influence of noise on wildlife.

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extracting sound data or monitoring seed removal. Ryan Kennedy and Pete Nylander were also instrumental in the field effort, working four and three years respectively. Having these two as knowledgeable and exceptional field assistants across multiple years was a blessing. Carolina Quintero has always been a supportive friend since day one in the bullpen and I owe several ideas that have led to my success to her. The collaboration and friendship with Juan Paritsis made Chapter VI of this dissertation possible.

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CHAPTER I

INTRODUCTION

EFFECTS OF NOISE ON WILDLIFE: LIMITATIONS AND CURRENT UNDERSTANDING

An increasingly important focus in ecology addresses how human disturbances influence biodiversity (*reviewed in* Fahrig 2003, Ewers & Didham 2006). Traditionally, ecologists have focused on how anthropogenic changes to native vegetation influence diversity and ecological processes (*reviewed in* Saunders et al. 1991), often overlooking other potentially influential components of human disturbance, such as anthropogenic noise. Research addressing the effects of noise on wild populations and communities is important for two main reasons. First, the relatively sudden rise of worldwide noise amplitudes is an evolutionary novel condition. Noise created by industrial machinery and vehicles is markedly different in frequency, more continuous, and often at much greater amplitudes, than sounds in most natural habitats (Slabbekoorn & Ripmeester 2008). Second, sound waves created by human noise can penetrate intact habitat located at great distances from the edge of physically converted lands (Forman 2000; Barber et al. 2010). Because few landscapes remain unaffected by humanity (Vitousek et al. 1997), there are few locations that are not exposed to these novel acoustic conditions. Yet despite the large potential influence noise may have on communities, we lack a basic understanding of how natural populations and communities respond to this common component of human disturbance; therefore, it is imperative that we begin to understand

how noise in human-altered habitats influences populations and communities. There are several recent, thorough reviews focused on how anthropogenic noise influences birds and other taxa (Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008; Barber et al. 2010); therefore, I do not provide a detailed review here. Instead, I briefly outline current knowledge in this quickly growing sub-discipline and highlight the main limitations from previous research efforts.

To date, the majority of studies aimed at understanding the consequences of noise exposure to wildlife have focused on birds, and with good reason; birds, more than any other vertebrate taxa, are especially well known for their vocal communication (Marler & Slabbekoorn 2004). Worries have grown that the widespread increases in anthropogenic noise exposure may functionally silence many birds (Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008), potentially altering population densities and entire avian communities. These concerns have been supported by a preponderance of correlative evidence showing reductions in abundances, occurrences and species richness near roads (e.g., van der Zande et al. 1980; Reijen et al. 1995; Reijnen et al. 1996; Kuitunen et al. 1998; Brotons & Herrando 2001; Forman et al. 2002; Ingelfinger & Anderson 2004; Peris & Pescador 2004; Palomino & Carrascal 2007; Delgado García 2008; Griffith et al. 2010). Because declines in birds are most severe in habitat near roadways, but declines are measurable even at large distances from high-traffic roads, authors of the majority of these studies have argued that traffic noise is the most probable explanation for declines. Additionally, because many birds depend on vocalizations to repel rivals (Krebs et al. 1981; McGregor et al. 1992) and attract mates

(Patricelli et al. 2002; Collins 2004), masking of these signals by noise provides a compelling mechanism that could account for these patterns. In other words, traffic noise may functionally silence many birds.

Unfortunately, as acknowledged by several of the authors cited above for the studies involving roads, evidence from these studies are suggestive at best, because several other mechanisms could represent dominant or partial factors responsible for the observed negative effect of roads on birds. For example, changes in habitat or edge effects may confound studies examining changes to bird densities or communities with distance from the roadway (Delgado García et al. 2008). Mortality of birds killed in collisions with vehicles could also account for these patterns (Kuitunen et al. 2003; Orlowski 2008) and vehicular motion and lights may also serve as stimuli that could result in declines in densities near roads (Pocock & Lawrence 2005). Finally, the factor that is most difficult to control is the influence of noise on researchers' abilities to detect birds (Pacifici et al. 2008). For instance, noise can reduce point count detections by approximately one-half, greatly biasing resulting estimates of species abundance and community-level metrics of diversity (Francis unpublished data).

Despite the limitations from studies aimed at examining population and community-level changes in response to noise, a separate but related line of investigation suggests that some species seem to cope well in noisy habitats via signal adjustments (*reviewed in* Brumm & Slabbekoorn 2005; Patricelli & Blickley 2006). Documented adjustments to noisy urban habitat conditions include a temporal shift to nocturnal activity in the European robin (*Erithacus rubecula*, Fuller et al. 2007) and a

noise-level dependent rise in signal amplitude in the nightingale (*Luscinia megarhynchos*, Brumm 2004). Upward shifts in song frequency in response to low-pitched traffic noise seem a particularly common strategy among urban birds. After this shift was first documented in the great tit (*Parus major*, Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006), evidence for shifts in other urban bird species is accumulating (Fernández-Juricic et al. 2005, Wood & Yezerinac 2006; Nemeth & Brumm 2009; Parris & Schneider 2009; Ripmeester et al. 2010). Real-time spectral adjustments in response to experimental noise exposure were recently documented for great tits (Halfwerk & Slabbekoorn 2009) and reed buntings (*Emberiza schoeniclus,* Gross et al. 2010), suggesting that these shifts are made via short-term behavioral adjustments.

Findings from these studies focused on signal modification in noise have led authors to argue that acoustic masking of communication signals may be an underlying mechanism responsible for reduced habitat use by birds in noisy areas and that those species most likely to suffer may be those with low frequency vocalizations that are most readily masked by low frequency industrial noise (Slabbekoorn & Peet 2003, Patricelli & Blickley 2006, Slabbekoorn and Ripmeester 2008). Rheindt (2003) provides the first evidence that acoustic masking of vocal communication may cause declines in bird populations; however, the results were limited due to complications associated road noise, lack of repetition and low statistical power (Slabbekoorn & Ripmeester 2008).

To rigorously test for a negative effect of noise on birds and to link declines to masking of acoustic signals by noise, a community-level study adopting a number of

critical controls is necessary. First, isolating noise as a single variable of interest is essential because it allows one to control for the many confounding stimuli that hinder interpretation of studies using road or urban noise (edge effects, changes in vegetation, visual stimuli of moving traffic, etc.). Second, because noise can severely hamper human observers' ability to locate birds (Pacifici et al. 2008; Ortega & Francis *in revision*), the ability to eliminate the influence of noise on detections is necessary. Finally, because avian vocalizations may vary in time (Luther & Baptista 2010), space (Kroodsma 2004), or in response to habitat structure (Ryan & Brenowitz 1985; Nemeth & Brumm 2009) and noise itself (Slabbekoorn & Peet 2003; Brumm & Slabbekoorn 2005), measurement of bird vocalizations from individuals in the same areas as measures of habitat use is also needed.

In this dissertation, I used a "natural experiment" that eliminated the influence of confounding factors common to noisy habitats and isolated noise as a single variable to determine whether noise negatively influences birds via acoustic masking and to explore the consequences of noise exposure on ecological communities.

STUDY DESIGN: AN UNCOMMON OPPORTUNITY

Energy extraction in remote locations provides an unexpected opportunity to isolate noise from confounding stimuli that co-vary with noise along roadways and in urban areas, and the work I present in this dissertation is not the only example of how researchers can use this opportunity. For example, Bayne and coworkers used energy sector infrastructure in Alberta, Canada to investigate the influence of compressor

station noise on bird densities (Bayne et al. 2008) and pairing success (Habib et al. 2007), but were unable to control for the influence of noise on detections in the study design. Here, I take a similar approach using gas well infrastructure in NE New Mexico, but control for the influence of noise on detections by turning off the noise. I provide a brief overview of the study area here, but give additional details regarding study sites, design and methodology in each chapter presenting new data (Chapters II through VI).

Study area

I conducted fieldwork for my dissertation within Rattlesnake Canyon Habitat Management Area (RCHMA), which is located in the San Juan Basin in northwestern New Mexico and managed by the Bureau of Land Management (BLM; Figure 1.1). RCHMA is dominated by piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands and is within one of the nation's most developed energy-producing regions (over 20,000 active oil and gas wells within the San Juan Basin, BLM 2003). Gas wells are often coupled with compressors, which aid in the transportation of gas through pipelines and run 24 hours a day, 365 days a year aside from periodic maintenance. These compressors generate low frequency noise at amplitude levels that are hazardous to humans (Habib et al. 2007; OSHA 2009). Because noisy compressors are present on some well pads (treatment sites) and absent on others (control sites; Figure 1.2), RCHMA provides a unique opportunity to determine the influence of noise on natural populations and communities. With the exception of background noise amplitudes, which is significantly higher on treatment sites than control sites through a

distance of 400 m from the compressor or wellhead (see Figure 2.5 in Chapter II), human activity and vegetation does not differ on and around well pads with and without noisy compressors that are used in this study (see Chapter II); thus, effects of noise are separated from other confounding variables that complicated previous attempts to characterize the influence of noise on wildlife.

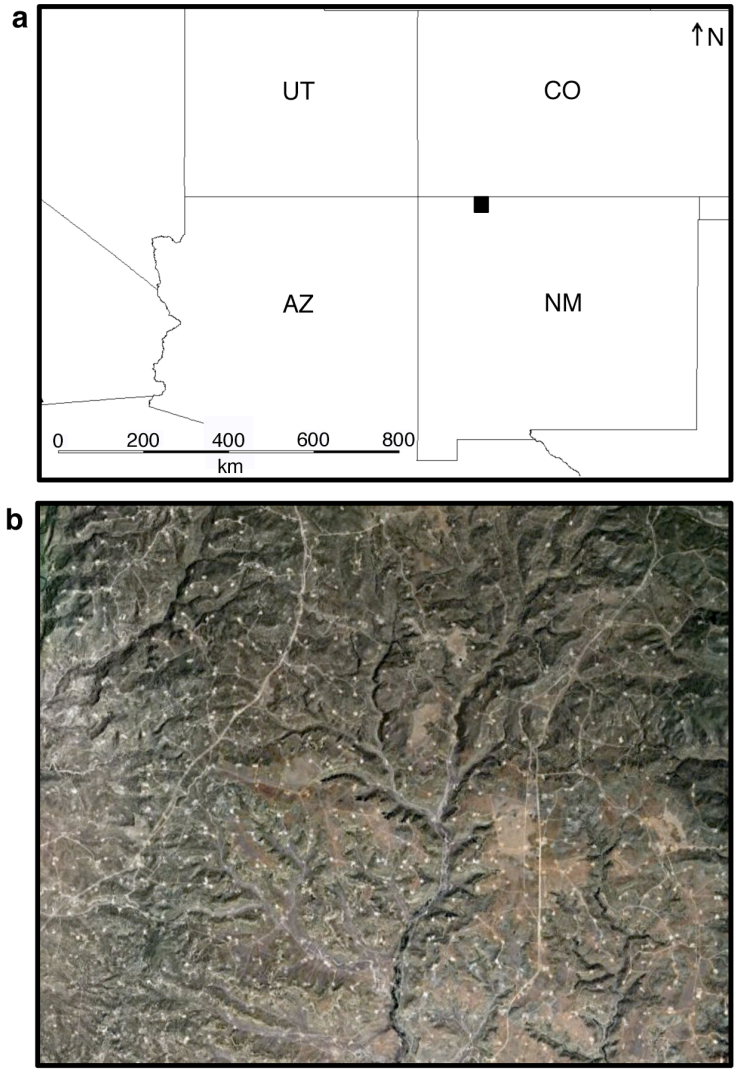


Figure 1.1 (a) Location of RCHMA denoted with a black square. (b) Sample image of a large area within RCHMA. Each light dot denotes a well pad with an active gas-producing well. Roughly half of the wells are coupled with compressors (image courtesy of GoogleEarth©).

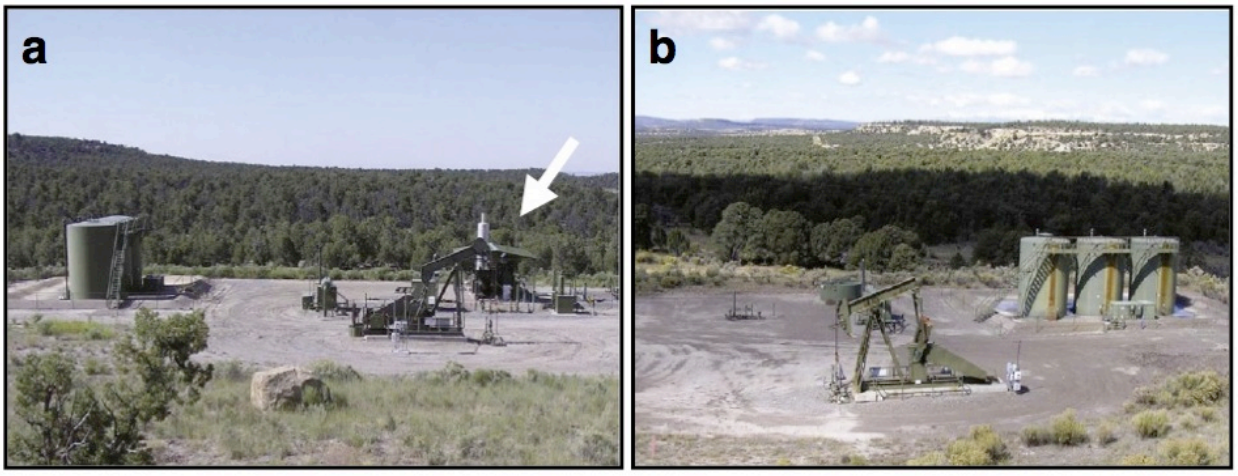


Figure 1.2 Two well pads and surrounding piñon-juniper habitat that were used in this study. Both photos illustrate gas well infrastructure associated with producing wells, but (a) has a noise-producing compressor (indicated by the white arrow) and was used as a treatment site and (b) lacked a compressor and was used as a control site.

SUMMARY OF CHAPTERS II THROUGH VI

Chapters II through VI were each prepared according to formatting styles of different peer-reviewed journals. Though I have made attempts to format the contents of this dissertation to be as consistent as possible, there are some noticeable differences among chapters, such as in the organization of sections within chapters, labeling of figures, and spelling of particular words (e.g., British vs. American English for "behaviour" vs. "behavior" respectively, or journal preferences for use of the "ñ" in words like "piñon" vs. "pinyon"). Finally, because others were involved in the acquisition of funding, study design, fieldwork and lab work, these chapters are written in first-person plural, reflecting their co-authorship.

Chapter II presents the strongest evidence to date that noise, in the absence of other stimuli, can change avian communities. In line with results from studies

investigating the effects of traffic noise on birds, species richness of nesting birds declines markedly in noisy habitats and the composition of nesting birds in quiet and noise areas are significantly dissimilar. Contrary to concerns that noise may reduce nesting success, nest success was higher in noisy habitat than in quiet habitat. This difference was due to decreases in predation by a major nest predator, the western scrub-jay (*Aphelocoma californica*), which had significantly lower occupancy rates in noisy areas. These results are published in the journal *Current Biology* with coauthors Catherine P. Ortega and Alexander Cruz and this chapter is formatted in the style of *Current Biology* reports.

Chapter III presents results from artificial nest predation experiments conducted over two breeding seasons to confirm results from real nests (Chapter II). Additionally, these experiments were conducted to determine whether predation risk differed between quiet and noisy habitat based on a decrease in predator abundance (numerical response) or because predators were present but noise interfered with their ability to locate nests (functional response, Chalfoun et al. 2002). In both seasons artificial nests in quiet habitat suffered greater predation than those in noisy habitat, confirming the pattern observed for real nests. Motion-triggered cameras paired with a random subset of artificial nests in the second year revealed that western scrub-jays were the most common predator and they were photographed depredating nests mainly in quiet habitat. This study was conducted in collaboration with Peter Nylander and Ryan Kennedy, who each used one season of data as their senior thesis projects at Fort Lewis College, and Catherine P. Ortega. All of these individuals are coauthors of the

resulting manuscript, which is currently in review for publication in an *Ornithological Monographs* issue focused on the influence of noise on birds.

Chapter IV presents compelling results that noise filters avian communities nonrandomly via masking of acoustic signals. I found support for the acoustic masking hypothesis from two separate sets of data: larger species with low frequency signals had negative responses to noise in their habitat use because their signals suffer from a greater degree of acoustic masking by noisy than smaller species with higher pitched signals. Other species-specific vocal characteristics, such as loudness and signal duration, failed to influence response to noise. These results corroborate a growing body of suggestive evidence that acoustic masking may drive species away from otherwise suitable habitat. This work was submitted to *Science* with coauthors Catherine P. Ortega and Alexander Cruz and appears formatted for *Science* in this dissertation.

Chapter V presents findings comparing habitat use and signal change in response to noise in two flycatcher species. Though species-specific vocal frequency and body size may generally predict habitat use in response to noise (Chapter IV), some species, such as the ash-throated flycatcher (*Myiarchus cinerascens*), which has fairly low frequency signals, increases the pitch of its songs and calls in noise and is uninfluenced by noise in terms of habitat use. In contrast, the gray flycatcher (*Empidonax wrightii*), which has a higher pitched song than the ash-throated flycatcher, does not change the frequency of its vocalization in response to noise, but its occupancy rate declines with increases in background noise. These results suggest that

noise-dependent signal modifications may be necessary for some species to cope with noise and raises important questions regarding the phylogenetic distribution of noise-dependent signaling capabilities. This work is in press in the journal *Proceedings of the Royal Society: Series B* with coauthors Catherine P. Ortega and Alexander Cruz.

Chapter VI presents a study using landscape patterns of gas well compressor noise to predict spatial patterns of avian habitat use and nest predation and evaluates how alternative management practices that reduce the spatial footprint of compressor noise may maintain “more natural” ecological patterns. The findings suggest that compressor noise can be mitigated quite well and maintain landscape-level patterns of habitat use and nest predation near values observed for quiet habitat on a smaller scale. This work was completed in collaboration with Juan Paritsis and is currently in review for inclusion in a special issue in the journal *Landscape Ecology* focused on soundscape ecology. Juan Paritsis, Catherine P. Ortega, and Alexander Cruz are coauthors.

CHAPTER II

NOISE POLLUTION CHANGES AVIAN COMMUNITIES AND SPECIES INTERACTIONS

ABSTRACT

Humans have drastically changed much of the world's acoustic background with anthropogenic sounds that are markedly different in pitch and amplitude than sounds in most natural habitats (Katti & Warren 2004; Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008). This novel acoustic background may be detrimental for many species, particularly birds (Slabbekoorn & Ripmeester 2008). We evaluated conservation concerns that noise limits bird distributions and reduces nesting success using a natural experiment to isolate the effects of noise from confounding stimuli and control for the effect of noise on observer detection biases (Pacifici et al. 2008). We show that noise alone reduces nesting species richness and leads to different avian communities. Contrary to expectations, noise indirectly facilitates reproductive success of individuals nesting in noisy areas due to the disruption of predator-prey interactions. The higher reproductive success for birds within noisy habitats may be a previously unrecognized factor that contributes to the success of urban-adapted species and loss of birds less tolerant of noise. Additionally, our findings suggest that noise can have cascading consequences for communities through altered species interactions. Given that noise pollution is becoming ubiquitous throughout much of the world, knowledge of species-specific responses to noise and the cumulative

effects of these novel acoustics may be crucial to understanding and managing human-altered landscapes.

Results and Discussion

Nearly anyone who has been near a busy roadway, an airport, or industrial equipment can attest to the intensity of sounds produced by human activities. Many of these anthropogenic sounds can be physically harmful or distracting to humans or wildlife and considered noise pollution (hereafter referred to as noise). Noise, characterized by high amplitudes and low spectral frequencies, is typical to habitats in and around human-altered landscapes (Forman & Alexander 1998; Katti & Warren 2004; Brumm & Slabbekoorn 2005; Patricelli & Blickley 2006; Reijnen & Foppen 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008). These acoustics have emerged swiftly on a global scale; therefore, noise presents an evolutionarily novel source of acoustic interference for many species and a potentially significant force influencing the ecology and evolution of many animals (Slabbekoorn & Ripmeester 2008). Because of their reliance on acoustic communication, birds have been viewed as especially vulnerable to the novel acoustics of noise (Slabbekoorn & Ripmeester 2008). Specifically, noise may disrupt acoustic communication, interfere with detection of warning signals, and elevate stress levels (Katti & Warren 2004; Brumm & Slabbekoorn 2005; Campo et al. 2005; Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008).

To date, noise has been associated with declining bird densities (Reijnen et al. 1995; Kuitunen 1998; Canaday & Rivadeneyra 2001; Forman et al. 2002; Bayne et al.

2008), prompting conservation concerns that many species may be excluded from otherwise suitable habitat due to ecologically sensitivities or intolerances to noise (Katti & Warren 2004; Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008). Additionally, individuals that settle in noisy habitats may have reduced reproductive success because noise interferes with detection of approaching predators (Warren et al. 2006; Slabbekoorn & Ripmeester 2008). Despite previous links between noise and bird declines, evidence demonstrating a direct negative influence of noise on birds has been equivocal because previous efforts have employed methods with insufficient controls over other stimuli associated with noise, such as the physical alteration of habitat, comparing communities from interior habitat to those on the edge, or visual disturbance of moving traffic or equipment (Warren et al. 2006; Dooling & Popper 2007; Slabbekoorn & Ripmeester 2008). These uncontrolled variables could also explain observed bird declines. Additionally, these studies have not accounted for the negative influence of noise on observer's ability to detect birds (Pacifici et al. 2008). We tested conservation concerns that noise results in declines in bird densities, community species richness, and reproductive success using a unique study design that controlled for the effects of stimuli often associated with noisy habitats and detection problems caused by noise. We show how noise, in the absence of other influential stimuli, can have either a negative, or an indirect positive effect on birds due to altered species interactions produced by species-specific responses to noise (Figure 2.1A).

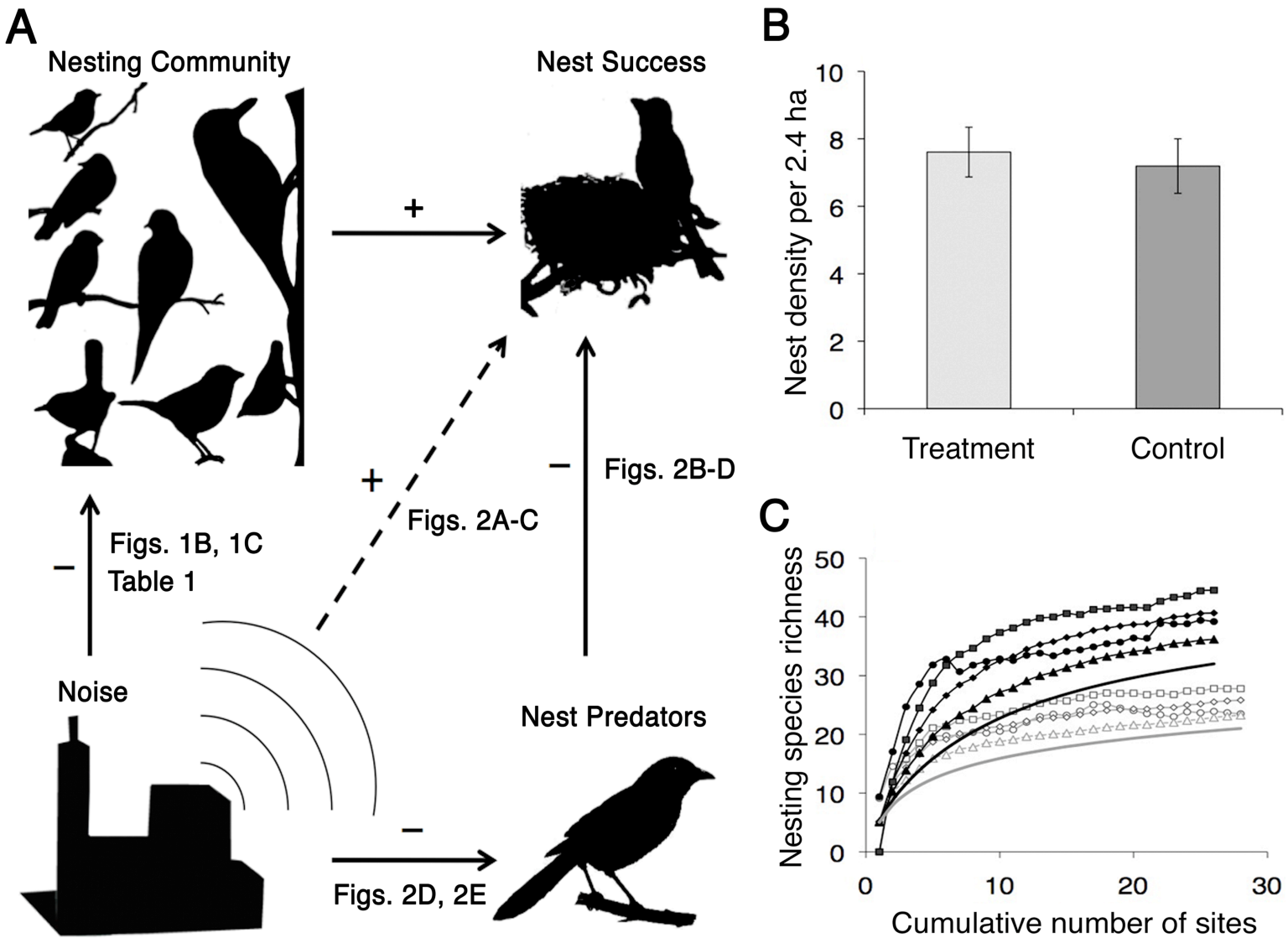

A
Nesting Community
Nest Success
+
+
Figs. 2A-C
–
Figs. 2B-D
–
Figs. 1B, 1C
Table 1
Noise
Nest Predators
–
Figs. 2D, 2E
B
Nest density per 2.4 ha
10
8
6
4
2
0
Treatment
Control
C
Nesting species richness
50
40
30
20
10
0
0
10
20
30
Cumulative number of sites

Figure 2.1 Influence of noise on nesting community, plus nest density and nesting richness on treatment and control sites. (A) Interaction web showing the pathway by which noise negatively influences species richness of the breeding community, but indirectly facilitates avian reproduction because fewer nests fail due to predation. The sign refers to the direction of the effect for each interaction. Figure and table numbers indicate which figure or table presents data supporting each pathway step. Noise negatively influences the nesting communities' species richness and a major nest predator, the western scrub-jay (*Aphelocoma californica*). Because the scrub-jay has reduced occupancy rates in noisy areas, fewer nests fail to predation. These changes brought about by noise result in an indirect positive effect on nest success (dashed line). (B) There was no difference in mean nest density between treatment and control sites. Results are shown as mean ± SEM. (C) Rarefaction and richness estimate curves reflected the observed difference in nesting species richness with higher estimates of nesting species richness on control sites (black lines and solid symbols) than treatment sites (gray lines and open symbols). Richness estimates are denoted as follows: solid line = rarefaction (Sobs), diamond = First-order Jackknife, square = Second-order Jackknife, circle = Chao 1, and triangle = bootstrap (see http://purl.oclc.org/estimates for explanations and calculations of estimators).

Nesting community richness and community composition

We located and monitored nests for three breeding seasons at our study sites among the scattered natural gas extraction infrastructure within pinyon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands of NW New Mexico. Our design provided a natural experiment that permitted isolation of noise as a single experimental stimulus. Treatment sites included woodland habitat adjacent to natural gas wells with noise-producing compressors, which aid in transportation of gas through pipelines and run 24 hours a day, 365 days a year aside from periodic maintenance and during our two-hour nest searching efforts and surveys. Woodland habitats adjacent to natural gas wells that lacked noise-generating compressors were used as control sites (see Supplemental Data section, Figure 2.3). We measured noise amplitudes at nests and throughout sites to characterize differences in the acoustic background between treatment and control

sites (see Supplemental Data section, Figures 2.4 and 2.5). Given that noise can reduce avian detection probabilities (Pacifici et al. 2008) and may hamper researcher ability to locate nests, we turned off all compressors (n = 9) during nest searching effort for the first two years of study and for half of all treatment sites (n = 5 turned off and n = 5 left on) in the third year.

Contrary to previous reports of reduced densities of birds due to road noise (Reijnen et al. 1995; Kuitunen 1998; Canaday & Rivadeneyra 2001; Forman et al. 2002; Peris & Pescador 2004), we found no difference in community nest density between treatment and control sites ($t = -0.38$, $df = 52$, $p > 0.70$; Figure 2.1B). Despite no difference in nest density, we observed 21 species nesting on treatment sites and 32 species nesting on control sites. Rarefaction and nesting species richness estimates from EstimateS, species richness estimation software (http://purl.oclc.org/estimates), supported the observed richness difference between the two site-types (Figure 2.1C). This difference was reflected by species that were unique to one of the two site-types: nests of 14 species were found only on control sites, yet nests of three species were found only on treatment sites.

In addition to the difference in richness between treatment and control sites, we detected clear differences in the composition of the nesting communities on each site-type. Analysis of similarity (ANOSIM) indicated that the nesting species composition on treatment and control sites was significantly dissimilar ($R = 0.19$, $p < 0.001$). This difference can be attributed to the difference in nesting species richness between noisy treatment and control sites, but also to the presence of indicator species for each site-

type (Dufrêne & Legendre 1997). The black-chinned hummingbird (*Archilochus alexandri*) and house finch (*Carpodacus mexicanus*) were strongly associated with treatment sites (Dufrêne-Legendre indicator species analysis: black-chinned hummingbird indicator value (IV) = 0.66, p = 0.001; house finch IV = 0.49, p = 0.001). This strong association is reflected by the relative abundance of each of these species on treatment sites: 36 (92%) of 39 black-chinned hummingbird nests and 29 (94%) of 31 house finch nests were on treatment sites. These species also accounted for a large proportion of the treatment site nesting community. Black-chinned hummingbird nests accounted for 17% and house finch nests accounted for 14% of all nests on treatment sites. In contrast, nests of these species were uncommon on control sites, each representing fewer than 3% of all control site nests. The mourning dove (*Zenaida macroura*) and black-headed grosbeak (*Pheucticus melanocephalus*) were strongly associated with control sites (mourning dove IV = 0.41, p = 0.001; black-headed grosbeak IV = 0.19, p = 0.025). Twenty-two (97%) of 23 mourning dove nests and all black-headed grosbeak nests (n = 5) were located on control sites. Mourning dove nests represented 12% and black-headed grosbeak nests represented 3% of the control site nesting community.

Besides the presence of noise, there were minor, albeit insignificant, differences between site-types in terms of number of pinyon trees and amount of bare ground (see Supplemental Data section, Table 2.2). These two variables had no affect on nesting patterns in terms of nest density or density of nesting species (see Supplemental Data section, Figure 2.6). There were no additional differences in habitat features between

treatment and control sites that would explain selection for treatment or control sites in each species' nest placement (see Supplemental Data section, Table 2.2).

We also detected avoidance of noise in terms of nest placement within treatment sites. Gray flycatchers (*Empidonax wrightii*), gray vireos (*Vireo vicinior),* black-throated gray warblers (*Dendroica nigrescens*), and spotted towhees (*Pipilo maculatus*) all nested significantly farther away from the well pad on treatment sites than control sites, suggesting avoidance of noise generated on treatment site well pads (Table 2.1). Nests parasitized by the brown-headed cowbird (*Molothrus ater*) were also significantly farther away from the well pad on treatment sites than control sites (Table 2.1). No species nested closer to the well pad on treatment sites than control sites.

Table 2.1 Species that nested significantly farther from the plot origin on treatment sites than control sites. Results presented as mean nest distance (m) from origin ± SEM.

Species	**Treatment**	**Control**	**t[a]**	**p**
Gray flycatcher (n=67)	261.6 ± 16.3	206.4 ± 14.7	2.51	0.015
Gray vireo (n=14)	275.3 ± 14.5	187.2 ± 33.8	2.40	0.043
Black-throated gray warbler (n=11)	285.7 ± 9.8	188.5 ± 24.8	3.66	0.006
Spotted towhee (n=33)	267.7 ± 25.3	157.4 ± 22.5	3.26	0.003
Cowbird parasitized nests (n = 21)	297.5 ± 22.1	171.7 ± 30.3	3.36	0.003
Nests of all species (n=400)[b]	221.6 ± 7.6	200.5 ± 7.7	1.96	0.052

[a] Two-tailed Welch two-sample t-test

[b] Nests of all species were pooled, uncorrected for number of nests for each species.

Our results confirm the conservation concern that noise negatively affects breeding bird communities through a reduction in nesting species richness, but the decline in richness was not reflected by a reduction in nest density of the breeding community as a whole. Rather, we documented a change in the composition of the community with species-specific responses to the noise disturbance that ranged from positive to negative, but predominantly negative. Although the negative influence of noise on birds has been implicated in a number of studies, findings have primarily been restricted to studies using surveys of individuals (Reijnen et al. 1995; Kuitunen 1998; Canaday & Rivadeneyra 2001; Forman et al. 2002; Rheindt 2003; Peris & Pescador 2004; Bayne et al. 2008), often under conditions in which evidence for the effect of noise on birds is weak due to effects of uncontrolled confounding stimuli or potential detection errors (but see Bayne et al. 2008 for analytical methods for dealing with differences in detection probability). Because we were able to control for the effects of other influential stimuli and detection biases, our results provide especially strong evidence that noise alone reduces habitat quality for numerous species. Yet two species were much more common on noisy treatment sites than control sites, prompting a need to identify whatever mechanism is causing the different responses among species.

In general, species-specific responses to noise remain poorly described and the mechanisms responsible for responses are largely unknown (Katti & Warren 2004; Brumm & Slabbekoorn 2005; Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008). Species' avoidance of noisy habitat may be due to ecological intolerances of noise or species' inability to effectively communicate through the din of

human activities (Rheindt 2003; Katti & Warren 2004; Brumm & Slabbekoorn 2005; Patricelli & Blickley 2006; Warren et al. 2006; Habib et al. 2007; Slabbekoorn & Ripmeester 2008). Vocal frequency characteristics of indicator species suggest that the latter may occur on our sites. The two control site indicator species have vocalizations characterized by low frequencies: mourning dove vocalizations have an emphasized frequency (frequency at which the vocalization has the highest amplitude) near 527 Hz (Tubaro & Mahler 1998) and black-headed grosbeak notes range from 1.5 and 4.0 kHz (Ritchison 1980). These frequency ranges overlap with most anthropogenic noise (< 2.0 kHz), and are within the frequency range of noise produced on treatment sites (< 5 kHz, see Supplemental Data section, Figure 2.4). Acoustic masking likely limits these species to control sites where their vocalizations can be heard. In contrast, treatment site indicator species have vocalization frequencies that may escape the masking effects of noise or are capable of adjusting vocal signals in response to noise. Black-chinned hummingbird vocalizations span 1.5-12.0 kHz, but generally have the most energy above 5 kHz (Rusch et al. 1996), and house finches are known to sing with higher minimum frequencies in response to urban noise (Fernández-Juricic et al. 2005). Signal adjustments may not permit house finches to escape masking effects of noise entirely, but could shift signals to higher frequencies at which compressor noise has less acoustic energy (see Supplemental Data section, Figure 2.4).

Signal plasticity or use of frequencies above those dominated by noise may facilitate black-chinned hummingbirds and house finches in their ability to inhabit noisy areas, yet these attributes do not explain each species' selection for treatment sites

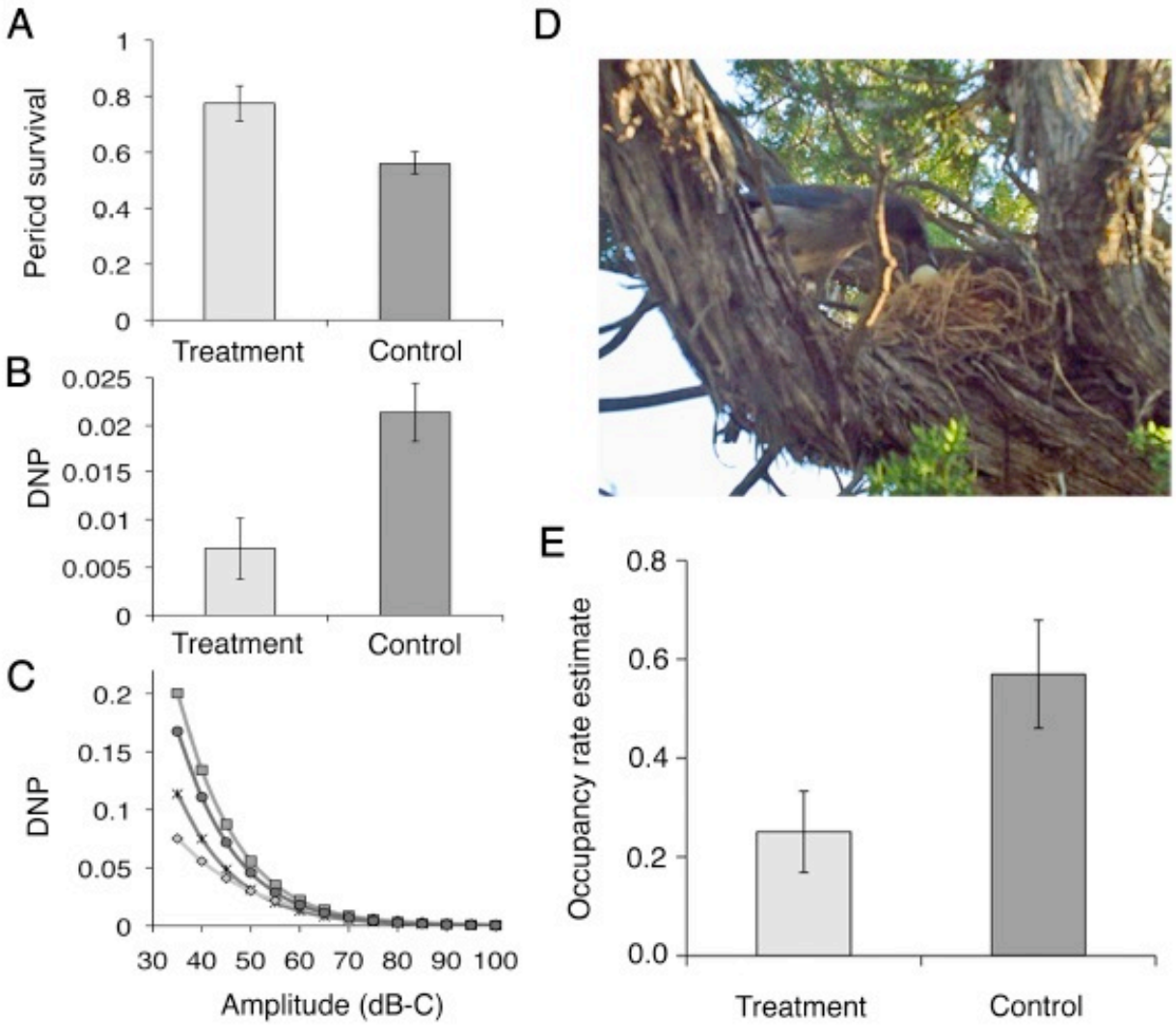
over control sites in their nest site selection. To our knowledge, this is the first evidence demonstrating that some species select for noisy habitats over quiet habitats and this finding provides an intriguing focus for future research. These species may use noise as a settlement cue in habitat selection; however, in light of our evidence documenting an altered community structure, plus higher nest success and lower levels of predation in noisy areas (see Influence of noise on nest success), the possibility exists that these species are responding indirectly to noise via factors such as lower interspecific competition pressure or additional cues representative of predation risk. Further research is needed to identify mechanisms responsible for settlement in noise areas, plus the potential tradeoffs associated with living in noisy conditions, such as declines in feeding rates (Quinn et al. 2006; Schaub et al. 2009).

Influence of noise on nest success

To determine whether noise negatively influences nest success we monitored all nests until they fledged or failed. Nest predation was the major cause of nest failure (76% of all failures) throughout the study area, followed by abandonment (13%) and brown-headed cowbird brood parasitism (9%). In terms of apparent (observed) nest success and counter to expectations, on treatment sites 13% of nests with known outcomes (n = 205) failed to predation, and 32% of nests with known fates (n = 174) were depredated on control sites ($\chi^2_1 = 12.1$, $p < 0.001$). We further estimated nest success in terms of daily nest survival (DNS), calculated using the logistic-exposure method (Shaffer 2004) and used likelihood-ratio tests to assess model performance. For the nesting community

as a whole, the DNS model with the inclusion of a site-type covariate was significantly better than a constant DNS model (likelihood-ratio test, $\chi^2_1 = 18.3$, $p < 0.001$). DNS was higher on treatment sites (0.989, 95% CI: 0.981 – 0.994) than control sites (0.974, 95% CI: 0.969 – 0.980; $\beta_{treatment} = 0.85 \pm 0.20$ SE), which reflected the difference in predation. Assuming a 23-day nest cycle, the predicted nest success from these DNS estimates was 22% higher on treatment sites than control sites (Figure 2.2A). Inclusion of those habitat features that differed slightly between treatment and control sites (amount of bare ground and number of pinyon trees) did not improve DNS model performance over the model with the site-type covariate (see Supplemental Data section).

Figure 2.2 Influence of noise on nest success, nest predation and a major nest predator, the western scrub-jay. (A) Predicted nest success from DNS estimates was higher on treatment sites than control sites for the entire nesting community. Error bars denote SE. (B) Daily nest predation (DNP, the inverse of DNS) was calculated using only nests with known outcomes that were successful or failed to predation (see Supplemental Data). DNP was higher on control sites than treatment sites. Results display DNP and SE. (C) Increases in noise amplitude decreased DNP for the nesting community and individual species that nested on treatment and control sites (community: DNS $\beta_{dB} = 0.092 \pm 0.02$ SE; gray flycatcher: DNS $\beta_{dB} = 0.06 \pm 0.04$ SE; spotted towhee: DNS $\beta_{dB} = 0.10 \pm 0.07$ SE; and chipping sparrow: DNS $\beta_{dB} = 0.10 \pm 0.045$ SE). Results are displayed as DNP. The asterisk denotes the nesting community; the diamond denotes the gray flycatcher; the square denotes the spotted towhee; and the circle denotes the chipping sparrow. We also used baited artificial nests paired with motion-triggered cameras to identify common nest predators. (D) Photograph of a western scrub-jay removing an egg from an artificial nest at one of our study sites. (E) The occupancy rate estimate for western scrub-jay was significantly lower on treatment sites than control sites. Results are reported as the proportion of point count stations occupied on treatment or control sites. Error bars denote SE.


A
Pericd survival
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0.2
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Treatment
Control
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DNP
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0.02
0.015
0.01
0.005
0
Treatment
Control
C
DNP
0.2
0.15
0.1
0.05
0
30 40 50 60 70 80 90 100
Amplitude (dB-C)
D
E
Occupancy rate estimate
0.8
0.6
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0.2
0.0
Treatment
Control

To more thoroughly examine the relationship between noise and nest predation, we estimated daily nest predation (DNP) by excluding all nests that failed for reasons other than predation and used only those nests that were successful or depredated. In this context, estimates of DNP were inverse measures of DNS. As expected, the DNP model including nest placement on treatment or control sites was an improvement over a constant DNP model (likelihood-ratio test, $\chi^2_1 = 27.0$, $p < 0.001$). DNP was much higher on control sites than treatment sites (Figure 2.2B). In other words, probability of not being depredated was higher on treatment sites than control sites (DNS $\beta_{treatment}$ = 1.14 ± 0.24 SE). Given that the composition of the breeding community differed on treatment and control sites, species-specific differences in DNP could potentially explain differences in nesting success between site-types; therefore, we also used measured noise amplitudes at each nest to predict DNP for three species common to treatment and control sites and for the entire community. DNP models including amplitude were significantly better than constant DNP models (likelihood-ratio tests, community: χ^2_1 = 30.6, $p < 0.001$; gray flycatcher: $\chi^2_1 = 7.0$, $p = 0.004$; spotted towhee: $\chi^2_1 = 3.5$, p = 0.04; and chipping sparrow (*Spizella passerina*): $\chi^2_1 = 4.2$, $p = 0.02$). Increases in noise amplitude resulted in lower DNP (i.e., probability of a nest escaping predation increased) for all three species and for the pooled nesting community (Figure 2.2C). These results suggest that higher nest success on treatment sites can be attributed to noise rather than different rates of nest success among species and that the difference is due to reduced nest predation with increased noise amplitudes.

Nest predator response to noise

To account for differences in nest predation between sites, we proposed that common nest predators were absent or less abundant on treatment sites than control sites. Using baited artificial nests paired with motion-triggered cameras we identified the western scrub-jay (*Aphelocoma californica*) as the primary nest predator in our study area (Figure 2.2D). To determine whether there was any evidence that noise influenced occupancy rates of this important nest predator we used standard point count surveys on treatment and control sites, with compressors turned off. We estimated scrub-jay occupancy using Presence occupancy modelling software and found the inclusion of a noise covariate (noise-conditional model) to significantly improve occupancy estimations over a uniform occupancy model (likelihood-ratio test, $\chi^2_1 = 17.3$, $p < 0.001$). Scrub-jay occupancy rates determined from the noise-conditional model were 32% higher on control sites than treatment sites (Figure 2.2E). This was the pattern we expected to see and supports the pattern of lower predation rates for nests on treatment sites.

Contrary to the concern that noise may negatively influence nest success (Warren et al. 2006; Slabbekoorn & Ripmeester 2008), our findings show that noise can have an indirect positive effect for individuals nesting in noisy areas. This result exemplifies the importance of examining the consequences of anthropogenic disturbance from a community-level perspective. In our study area the decrease in nest predation was due to the western scrub-jay's avoidance of noisy habitat. Scrub-jay's intolerance of noisy habitat, much like the control site indicator species, may be due to acoustic masking of its vocalizations, which include frequencies below 2 kHz (Curry et al. 2002). Future

research should consider the possibility that nest predators present in noisy areas, especially those that rely on acoustic cues to locate nests, may be less likely to locate nests due to the masking effects of noise, which would also lead to increased nest success with noise amplitude.

That noise changes patterns of nest predation has important implications for additional species interactions in noisy landscapes. For example, in our study area the scrub-jay is not only a major nest predator, it is also a key mobile link for pinyon pine through dispersal of its seeds (Vander Wall & Balda 1981; Chambers et al. 1999). Scrub-jay avoidance of noisy habitats may have negative consequences for seedling recruitment that could result in decreased pinyon pine densities in noisy areas, potentially affecting many organisms and community dynamics that are dependent on pinyon pine (Brown et al. 2001; Mueller et al. 2005). The full extent to which noise can trigger changes is urgently needed given the rate at which natural habitat is transformed by human activities. Most insight on the cumulative consequences of noise pollution may be gained through studies that focus on species with important roles within communities across diverse habitat types.

CONCLUSIONS

The current study has important implications for both avian conservation and community ecology within human-altered landscapes. The change in the avian community is in line with earlier studies implicating the negative influence of noise on birds (Reijnen et al. 1995; Kuitunen 1998; Canday & Rivadeneyra 2001; Forman et al. 2002; Reijnen &

Foppen 2006; Bayne et al. 2008); however, we provide the first evidence of this trend while simultaneously controlling for confounding stimuli and potential noise-caused detection biases. This is the strongest evidence to date that noise negatively influences bird populations and communities, and acoustic masking may be a dominant mechanism precluding many birds from breeding in noisy habitats (Rheindt 2003; Slabbekoorn & Peet 2003; Katti & Warren 2004; Patricelli & Blickley 2006; Slabbekoorn & den Boer-Visser 2006; Warren et al. 2006; Habib et al. 2007; Slabbekoorn & Ripmeester 2008). Because noise also indirectly facilitates reproductive success, species intolerant of noise may suffer not only from exclusion from noisy habitats that may be otherwise suitable, but also suffer higher rates of nest predation relative to species inhabiting noisy areas. If this phenomenon is common to noisy environments, it may help explain the high degree of success among urban-adapted species and the homogenization of avian communities in and around human-altered habitats (Slabbekoorn & den Boer-Visser 2006; Clergeau et al. 2006). Perhaps more noteworthy, however, is that noise alone can disrupt species interactions, potentially influencing many organisms and processes indirectly. Noise pollution is only becoming more prevalent throughout much of the world. Knowledge of how species respond to this novel force, and especially those with critical links within the ecosystem, may be crucial to maintaining biodiversity and ecological processes in the growing number of landscapes disrupted by our industrial clamour.

SUPPLEMENTAL DATA

Study Sites

All fieldwork for this study was carried out in Rattlesnake Canyon Habitat Management Area (RCHMA), in NW New Mexico during the breeding seasons of 2005-2007 (Figure 2.3). In 2005-2006, we used nine control sites and nine treatment sites; in 2007, we used eight control sites and 10 treatment sites (each measured 400 m × 60 m (2.4 ha); Figure 2.3). Gas well pads with and without compressors were the same size. Plot direction was selected randomly, provided that it included appropriate pinyon-juniper habitat and traversable terrain. In 2006, we replaced two control sites and one treatment site used in 2005 with new sites due to the difficulty of accessing the replaced sites during our scheduled visits to all other sites. In 2007, we could not use two control sites used in 2006 because new wells with compressors had been constructed nearby, which elevated the noise amplitude on these sites. One new control site and one new treatment site was added in 2007.

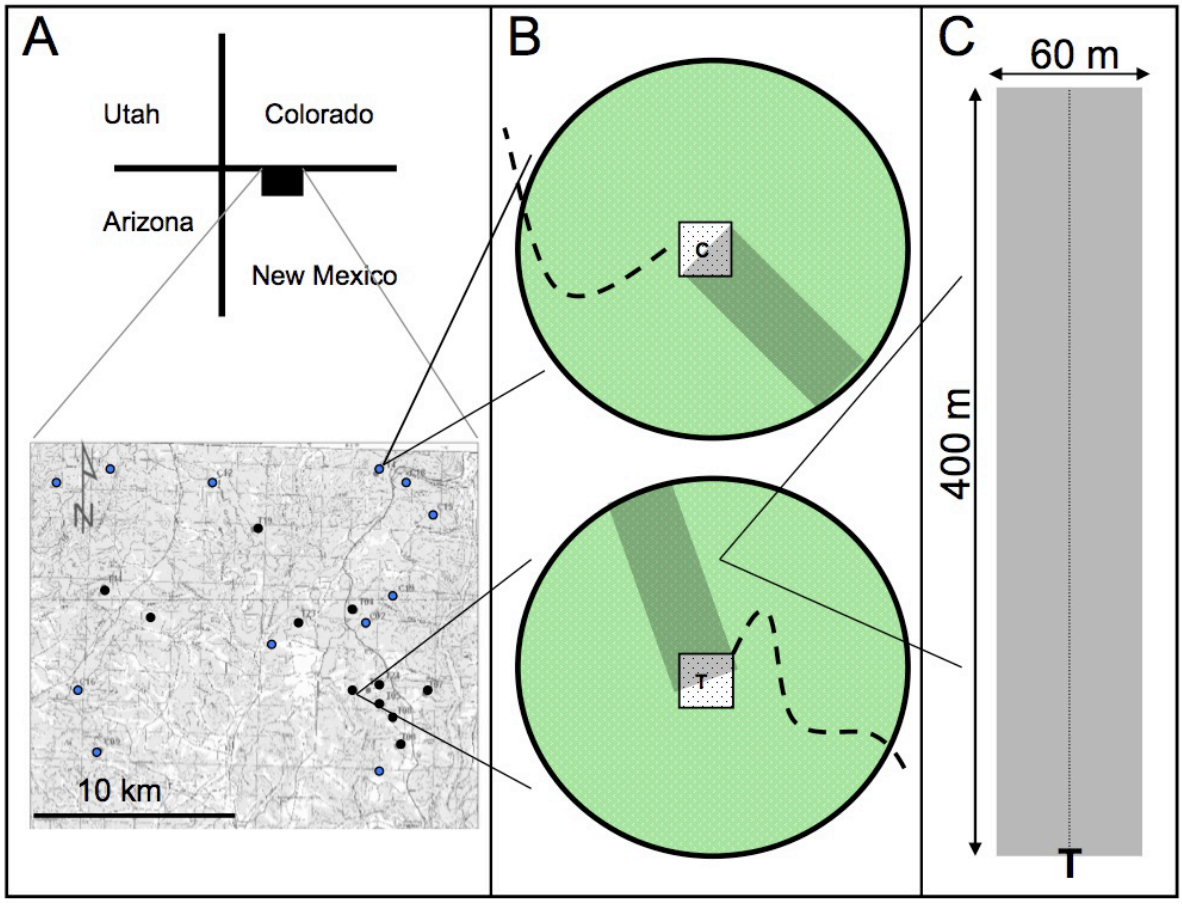


Figure 2.3 (A) RCHMA is located in NW New Mexico. Dots on map denote noisy treatment sites (black) and control sites (blue). (B) Study sites originated on well pads (light squares) without compressors (letter C) as control sites, or with compressors (letter T) as treatment sites. Dashed lines represent access roads. (C) Nest searching transects were 2.4 ha in area, measuring 400 x 60 m.

Nest Searches

During nest searches, in 2005 and 2006 compressors were shut down during our site visits to eliminate biased results, particularly nest density, because researchers rely heavily on avian alarm calls to detect birds at or near their nests. During 2007, however, five compressors were shut down during our visits so that we could evaluate the influence of noise on our ability to locate nests. Therefore, we included five treatment

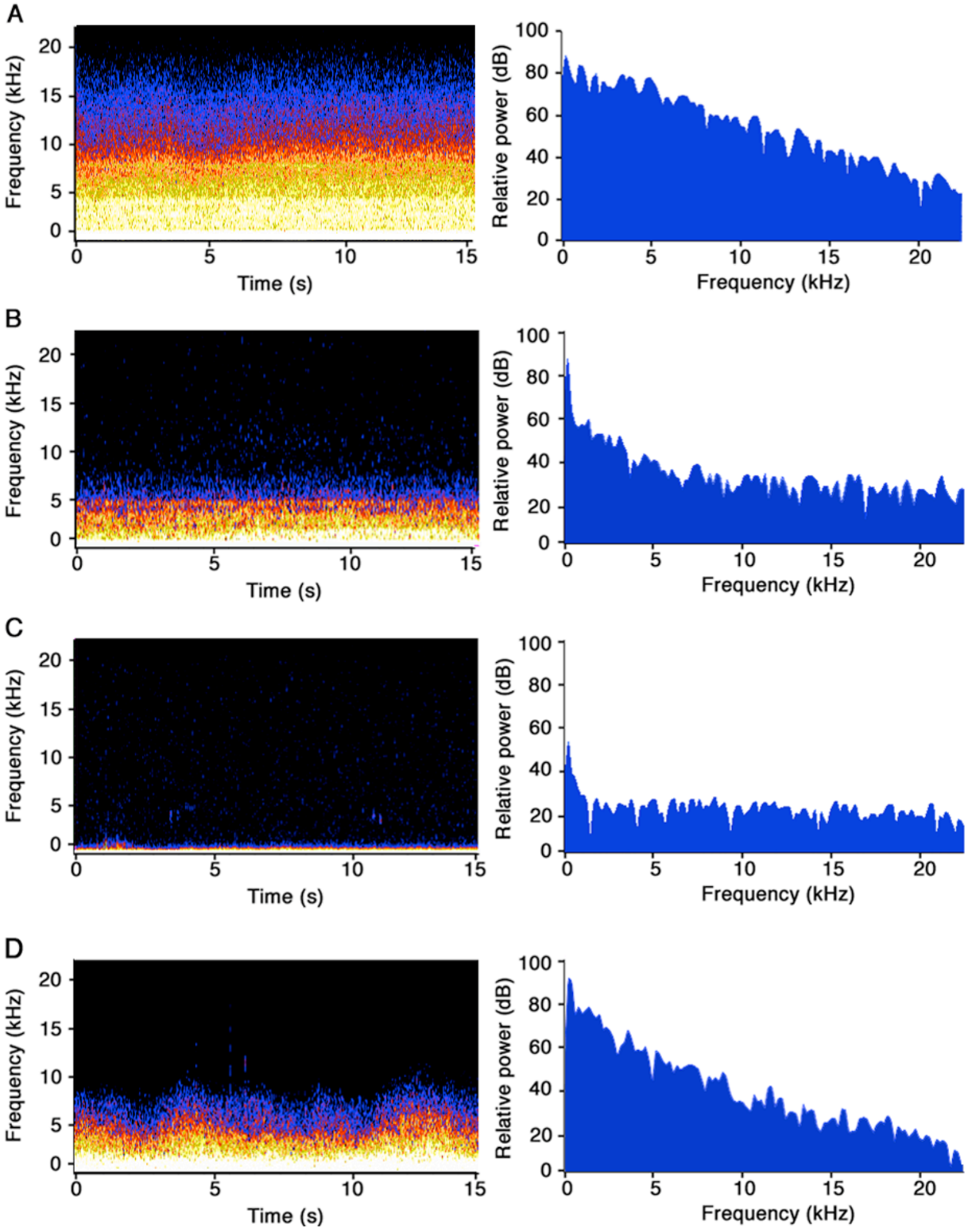
sites with compressors shut down and five treatment sites with compressors running during our visits. We visited each site every 3-5 days to search for and monitor nests. The time of day of each site visit and all observers were systematically rotated throughout all sites such that each site received equal effort by each observer during different times of the day.

Noise Measurements

Noise amplitude measurements were taken with NIST certified sound pressure meters (Casella® model CEL 320 and CEL 1002 converter) at 987 locations (all nests and 50 m incremental distances from compressors or well head) on three separate days in 2005 and 2006 and on two separate days in 2007 to control for environmental variability. Measurements were not taken when wind conditions exceeded 16 km/h. At each location we measured amplitude with A- and C-weighting. Because the compressor noise had the most acoustic energy at low frequencies (Figure 2.4) we used C-weighted (dB-C) values in all analyses because C-weighting provides a better representation of acoustic energy across most frequencies and filters less low frequency noise than A-weighting. Mean sound pressure levels recorded for individual measurements were used to calculate an overall mean sound pressure level for each location and used for analysis. Ambient noise frequencies were recorded for all sites with an Audio-Technica AT815b microphone with a 30 Hz to 20,000 Hz frequency response. The spectral composition of compressor noise near the compressor (20 m) was predominantly located between 0 and 5000 Hz, but had considerable energy as high as 10,000 Hz

(Figure 2.4A). Noise at higher frequencies attenuated more quickly with distance from the compressor than low frequency noise (Figure 2.4B). The attenuation of high frequencies resulted in a noise disturbance similar in frequency to noise found along roadways and in urban habitats (Figure 2.4; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006). Despite the attenuation of high frequencies, noise amplitude (dB-C) was significantly higher on treatment sites than control sites through 400 m from site origins (two-sample t-test: $t = 3.8$, $df = 21$, $p < 0.001$, Figure 2.5).

Figure 2.4 Spectrogram (left) and power spectrum (right) examples of background noise on a treatment site at 20 m from the compressor (A), 200 m from the compressor at the mid-point of each site (B), on a control site 20 m from the wellhead (C), and an example of road noise (D), measured 50 m from a four lane undivided highway at midday. Warmer colors in the spectrograms indicate more acoustic energy located at those frequencies, which is reflected by higher amplitude values in the power spectra. Comparison of A and B show that much of the noise above 5 kHz that had considerable relative power near the compressor (A) had attenuated (lost power) at a distance of 200 m from the compressor (B).


A
B
C
D
Frequency (kHz)
Time (s)
Relative power (dB)
Frequency (kHz)
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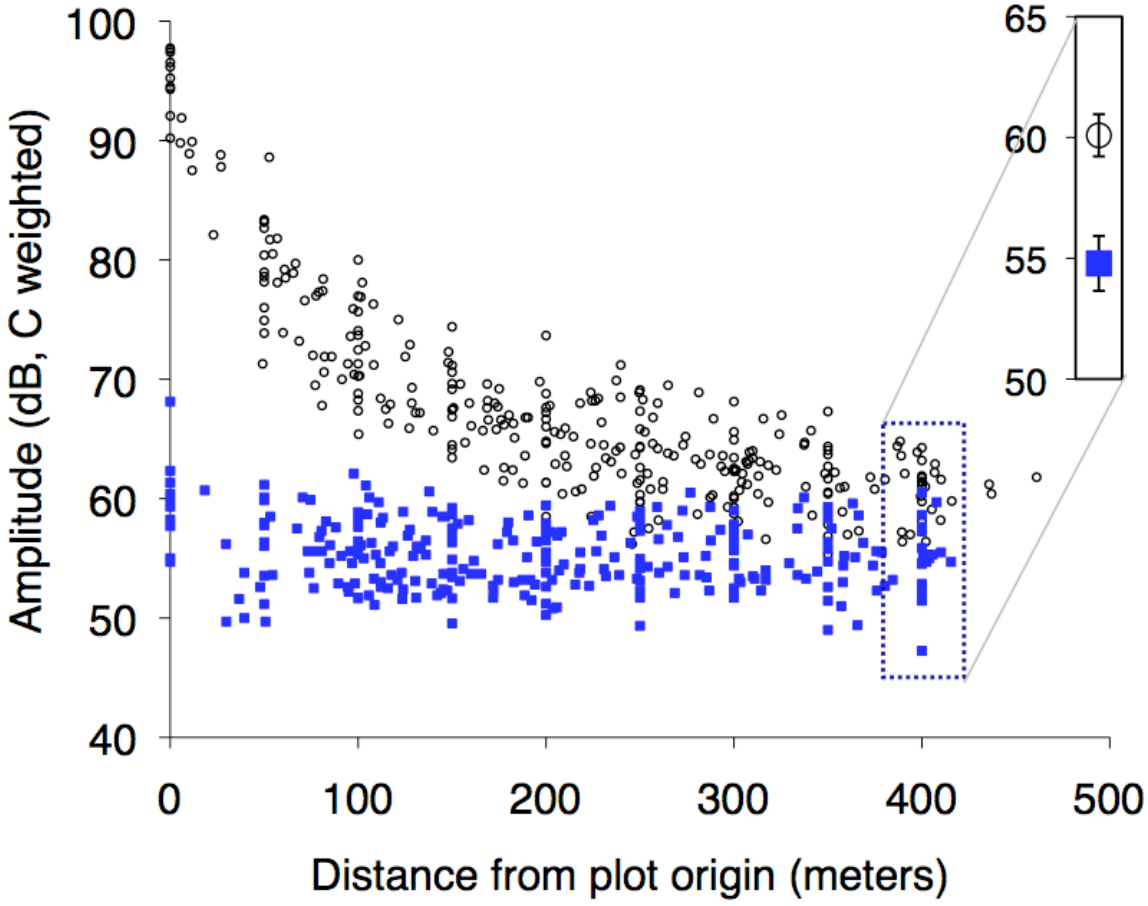


Figure 2.5 Amplitude (dB-C) on treatment sites (open circles) and control sites (blue squares). Noise amplitude was significantly higher on treatment sites than control sites throughout the study sites. On inset at 400 m, results are presented as means ± SEM.

Habitat Assessment

In order to determine whether there were any differences in habitat, besides the presence of noise on treatment sites, that might influence patterns in nesting or nest predation, we measured habitat information at each site with a modified Breeding Bird Protocol (Martin et al. 1997). At each site we collected habitat information on 25 m diameter vegetation plots (≈ 490 m^2). Plots used to compare vegetation between treatment and control sites were standardized at 100m and 300m along the mid-line of the 400 × 60 m nest study sites.

At each plot, two 50-m tapes were placed on the ground at 90^o angles, intersecting at the plot center; these represented ground and canopy transects. Starting at point 0 and extending to 25 m, at each meter along the tape (26 points for each transect, 52 total points for each plot), we determined ground cover (bare ground, rock, live matter, dead wood [including logs > 5 cm diameter, roots, and stumps], and non-organic matter). We categorized all live matter as grass/forb, shrub, or tree, and identified each to species where feasible. We measured the height of each plant along the ground transects where the plant intersected the vertical plane of the point on the tape. For dead matter, we measured litter depth. At each meter along the two transects, we also determined presence or absence of canopy (≥ 1 m). The tapes divided plots into quadrants. In each quadrant, we counted and identified to species all trees and shrubs > 50 cm, noting whether they were alive or dead. Mean values from the two vegetation plots at each site were used in analysis for differences in 13 habitat features

between treatment and control sites. Significance threshold for comparisons of 13 habitat features was adjusted to 0.0038 to correct for multiple comparisons.

There was no difference between treatment and control sites in 13 habitat features that we considered (Table 2.2). There were, however, two minor, but insignificant differences in habitat between the two sites: treatment sites had a more bare ground and fewer pinyon trees than control sites. Due to the presence of these minor differences, we also evaluated the influence of each on nesting patterns and nesting success (see *Nesting Density, Species Richness and Community Composition* and *Nest Success* sections).

Nesting Density, Species Richness and Community Composition

During the breeding seasons of 2005-2007 we located and monitored a total of 400 nests of 35 species: 213 nests of 21 species on treatment sites and 187 nests of 32 species on control sites. In our analysis of nest density, nesting species richness and community composition we used single nests as the unit of observation. Nest density was similar between treatment and control sites (Figure 2.1B). We also tested for differences in density of nesting pairs on treatment and control sites by excluding multiple nests within single territories by multiple brooded species and all probable renesting attempts following nest failure. Density of nesting pairs also did not differ on treatment (7.29 ± 0.69 SEM) and control sites (6.73 ± 0.73 SEM; two sample t-test: $t = 0.55$, $df = 52$, $p = 0.58$).

Table 2.2 No difference in habitat features at control and treatment sites.

Habitat Feature	Treatment	Control	df	t[c]	p
Canopy cover[a]	15.55 ± 1.41	18.48 ± 1.52	21.00	1.38	0.18
Bare ground[a]	11.96 ± 1.39	8.71 ± 1.01	18.12	1.83	0.08
Live matter[a]	13.82 ± 2.53	13.44 ± 1.85	18.24	0.12	0.91
Rock[a]	3.83 ± 1.73	5.75 ± 1.38	19.19	0.85	0.41
Dead wood[a]	0.92 ± 0.23	1.45 ± 0.41	17.64	1.13	0.27
Grasses/forbs[a]	8.67 ± 2.21	4.81 ± 1.53	17.58	1.39	0.18
Litter depth (cm)	8.12 ± 1.57	7.81 ± 1.47	20.48	0.14	0.89
Juniper trees[b]	12.12 ± 2.26	9.02 ± 1.27	15.48	1.15	0.27
Dead junipers trees[b]	1.05 ± 0.26	0.73 ± 0.28	21.00	0.80	0.43
Pinyon trees[b]	6.89 ± 1.13	12.73 ± 2.89	14.55	1.87	0.08
Dead pinyon trees[b]	4.73 ± 1.19	4.65 ± 1.10	20.44	0.05	0.96
Shrubs[b]	50.17 ± 9.71	42.94 ± 6.58	17.39	0.60	0.56
Total trees[b]	19.01 ± 2.94	21.75 ± 2.71	20.39	0.67	0.51

Results presented as mean ± SEM.

[a] Transect point counts (52 total points per plot)

[b] Total per 490.6 m^2

[c] Two-sample t-tests. No two-tailed t values were significant at $\alpha = 0.05$ when Bonferroni corrected to $P \leq 0.0038$ across 13 comparisons and without correction for multiple comparisons.

Due to the slight differences between treatment and control sites with respect to amount of bare ground and number of pinyon trees, we used regression to evaluate the influence of each on nest density and nesting species density (number of nesting species per 2.4 ha site). We used the mean values for each habitat feature from each site (see Habitat Assessment) as predictor variables. For nest density and nesting species density we used mean values for each site. Each value was calculated as the sum divided by the number of years each site was used in the study. There was no evidence that bare ground influenced nest density ($R^2 = 0.03$, $F_{1,21} = 0.45$, $p = 0.51$) or nesting species density ($R^2 = 0.02$, $F_{1,21} = 0.56$, $p = 0.46$; Figures 2.6A and 2.6B). Similarly, number of pinyon trees at each site had little influence on nest density ($R^2 = 0.02$, $F_{1,21} = 0.50$, $p = 0.49$) or nesting species density ($R^2 = 0.03$, $F_{1,21} = 1.57$, $p = 0.22$; Figures 2.6C and 2.6D). Because these habitat features appear not to influence nesting patterns, the observed differences between site types likely reflect the influence of noise pollution.

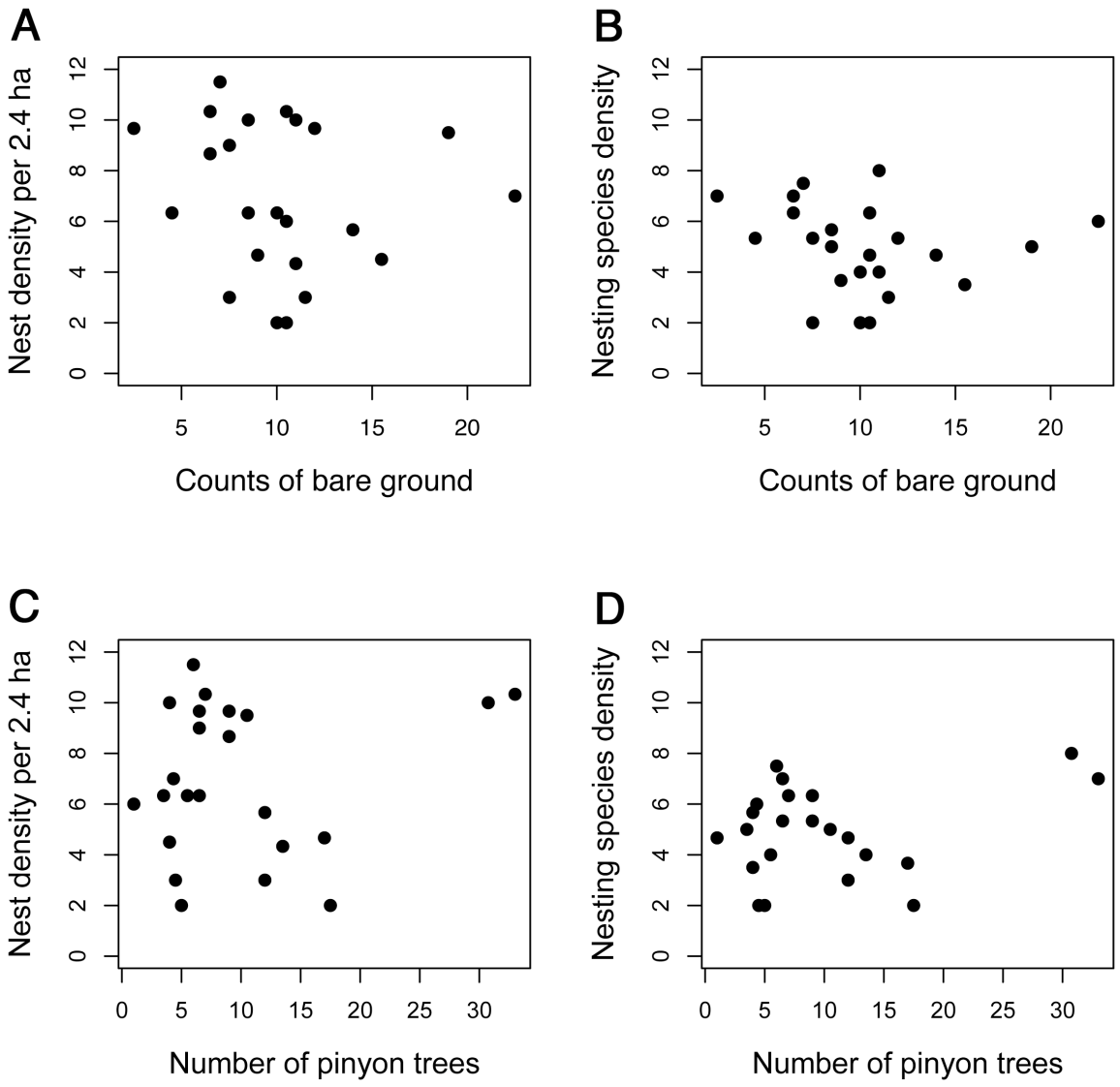


Figure 2.6 (A and B) Amount of bare ground at each site (calculated as number of transect point counts out of 52 points total per 490.6 m^2 vegetation plot) had an insignificant influence on nest density per site (A) and density of nesting species (B). (C and D) Number of pinyon trees at each site (calculated as number of pinyon trees per 490.6 m^2 vegetation plot) also had an insignificant influence on nest density per site (C) and density of nesting species (D). Results are displayed as the mean nest density and mean nesting species richness per site.

In 2007 half of the compressors on treatment sites (n=10) were turned off during nest searching efforts, which permitted us to evaluate the influence of noise on observer ability to locate nests. Counter to expectations, the number of nests located on treatment sites with the compressor left on (12.00 ± 2.35 SEM) did not differ to those sites with compressors turned off (9.00 ± 1.67 SEM; two sample t-test: $t = 1.04$, $df = 8$, $p = 0.33$). This result provided evidence that the presence of noise did not negatively affect our ability to locate nests; however, the finding was at odds with the known negative impact of noise on observer detection of birds using point counts (Pacifici et al. 2008). This discrepancy may be explained by a fundamental difference in effort required by nest searching and point count methods. For example, in each year we logged over 100 man-hours at each site intensively searching for nests. This repeated effort provided numerous opportunities to locate nests that may have escaped detection on an earlier search effort due to the masking of alarm calls emitted by nesting individuals. In contrast, standard point count surveys, in which individuals are counted from fixed line transects (Fernández-Juricic et al. 2005; Bock et al. 2008) or points (Bayne et al. 2008), may sum to only a few survey hours for a single transect or point, leaving fewer repeat opportunities to detect birds that may have been missed due to the masking effects of noise on initial surveys. Still, we caution that the absence of an effect of noise on nest detection was based on a small sample size from a single breeding season. Obtaining definitive evidence regarding the influence of noise on nest detection would require a more rigorous effort. Study designs that control for habitat variability by using each site as its own control and experimentally introducing or removing the noise disturbance

between breeding seasons would provide especially convincing evidence for or against the negative influence of noise on nest detection.

Nesting species richness was higher on control sites than treatment sites in each season. To compare species richness between the two site-types we pooled data from each season to create treatment and control rarefaction curves and richness estimators in EstimateS, species richness estimation software. We used 100 randomizations of sample order for all estimates.

To test for differences in species composition between treatment and control sites we calculated Bray-Curtis similarity coefficients across all sites. We used analysis of similarity (ANOSIM) to compare the level of similarity among sites of a site-type (treatment or control) to that among all sites. To identify particular species characteristic of treatment or control sites we used Dufrêne-Legendre indicator species analysis (Dufrêne & Legendre 1997), which uses species relative frequencies and abundances on treatment and control sites to calculate an indicator values for each species. An indicator value of 100 for a given site-type would indicate that a species was recorded in each sample for that site-type and was not observed in any samples from a different site-type. To assess significance of indicator values we used Monte Carlo randomizations that assigned alternate indicator values for the same data randomly assigned to treatment or control sites. Finally, we also assessed species' avoidance of noisy habitat within treatment sites by comparing the distance from the well pad at which species nested on treatment and control sites using two-sample t-tests (Table 2.1).

Nest Success

Of 400 monitored nests, 379 nests had known outcomes and were used to analyze daily nest success (DNS) per nesting attempt with the logistic-exposure method (Shaffer 2004). These nests were exposed for a total of 6,661 days. For daily nest predation (DNP; the inverse of DNS) estimates, we used all nests that were successful or failed due to predation (n = 348), which were exposed for a total of 6,301 days. We also estimated DNP for individual species and the community using noise amplitude at the nest to estimate DNP. Gray flycatcher DNP estimates were calculated with a total of 1139 days of exposure from 60 nests. Chipping sparrow DNP was analyzed with 64 nests and 888 days of exposure. DNP estimates for spotted towhees included 32 nests exposed for a total of 341 days. Nests were considered successful if ≥ 1 nestling fledged. We used likelihood-ratio tests to determine whether there was evidence that nest placement on treatment or control sites or noise amplitude at the nest influenced DNS or DNP.

On account of the minor differences between treatment and control sites in terms of number of pinyon trees and amount of bare ground per site, we also evaluated the influence of each on nest success. We added each variable to the DNS model including the site-type covariate (nest placement on a treatment or control sites) and used likelihood-ratio tests to assess whether inclusion of each additional predictor variable, or both, improved model performance. Addition of each variable failed to improve the site-type covariate DNS model for the nesting community as a whole (likelihood-ratio tests: number of pinyon trees covariate, $\chi^2_1 = 0.7$, $p = 0.35$; bare ground covariate, $\chi^2_1 = 1.7$, p

= 0.14; number of pinyon trees and bare ground covariates, $\chi^2_2 = 2.6$, $p = 0.13$). Because the inclusion of these habitat features did not improve the DNS model performance, noise pollution is likely the dominant factor accounting for differences in nest success on treatment and control sites.

Artificial Nest Experiments

We used artificial nests baited with Japanese quail (*Coturnix coturnix*) eggs to identify major nest predators within our study system. In 2007, 25 artificial nests were placed at each of three study plots for both treatment and control sites (150 nests total) at randomly selected points located between a distance of 50 m and 125 m from the wellhead or compressor. At each random point, nests were placed in the closest juniper tree at a height of ≈ 2 m. Artificial nests were canary nests tightly wrapped with gray wood excelsior material to simulate gray flycatcher nests. At 10 randomly selected nests on control and treatment sites (20 total), we placed motion-triggered digital cameras focused on the nest. When a nest with a camera was depredated, we moved the camera to another randomly selected nest. Nests were checked for signs of predation on every fourth day (from initial egg placement) for three visits. Predation was considered to be any sign of egg puncture or disappearance of one or more eggs.

We obtained photographs of predators at six of the 20 artificial nests paired with cameras. We obtained photographs of scrub-jays depredating four nests, a least chipmunk (*Tamias minimus*) depredating one nest, and a Steller's jay (*Cyanocitta stelleri*) depredating one nest.

Western Scrub-jay Surveys and Occupancy

In 2007 we conducted surveys for western scrub-jays at eight control sites and five treatment sites with compressors turned off during our surveys. All wells included in the nest study were also used for surveys. Within two concentric circles around each well (50 m from the well and 125 m from the well), we surveyed 16 randomly generated point count locations. Each point count location was visited twice during the study. At each point count location, we conducted a seven-minute bird survey, and all surveys were completed between 7:00 and 12:00. Using Presence occupancy modelling software, we estimated occupancy rates of scrub-jays on treatment and control sites. We assumed a constant detection probability on all surveys because there were no systematic differences between treatment and control site habitat features (Table 2.2) and compressor noise was turned off during surveys on treatment sites as to not bias our ability to locate birds. We used a likelihood-ratio test to compare two models: a model assuming uniform occupancy rates across all point count stations (null) and a model with conditional occupancy rates that were dependent on site-type (i.e., point count stations on treatment or control sites).

CHAPTER III

ANTHROPOGENIC NOISE AND NEST PREDATORS: ARE PREDATORS UNABLE TO LOCATE NESTS OR ARE THEY ABSENT FROM NOISY AREAS?

ABSTRACT

A leading conservation concern involving the influence of anthropogenic noise on birds has been that individuals breeding in noisy habitats may have reduced reproductive success. In contrast to this concern, we recently found that increases in anthropogenic noise amplitude positively influenced nest survival through a decrease in nest predation. Based on this result, we hypothesized that anthropogenic noise may either result in (1) a numerical decrease in predators in noisy areas, and/or, (2) a functional predator response, in which predators are present, but noise interferes with their ability to locate nests. We separated the effects of nest predation risk due to a numerical decrease in predators and risk associated with activity at the nest using artificial nest experiments on quiet control sites and noisy treatment sites and within a broad range of noise exposure. Our results concurred with results from real nests regarding patterns of predation, suggesting that common predators may have reduced abundances in noisy areas and with increased noise exposure. Cameras paired with artificial nests photographed Western Scrub-jays (*Aphelocoma californica)* depredating nest contents mainly on quiet control sites. Our findings suggest that breeding bird communities in

areas with high amplitudes of anthropogenic noise may benefit from increased nest success. However, this benefit should be viewed in the context of known changes to avian nesting community diversity when exposed to anthropogenic noise; only those species tolerant of noise may thrive in these noisy habitats.

INTRODUCTION

Anthropogenic noise is pervasive in urban areas, along roadways, and even in rural areas influenced by industrial activities (Bayne et al. 2008, Francis et al. 2009, Barber et al. 2010). Recently, anthropogenic noise has been implicated in the decline of bird densities (Reijnen et al. 1995, Kuitunen 1998, Canaday & Rivadeneyra 2001, Forman et al. 2002, Bayne et al. 2008) and shown to negatively influence avian nesting community diversity (Francis et al. 2009). These patterns may be due to species-specific intolerances to anthropogenic noise (Patricelli & Blickley 2006, Warren et al. 2006, Slabbekoorn & Ripmeester 2008, Francis et al. 2009), but may also be due to demographic processes, such as reduced reproductive success for individuals nesting in noisy areas. Investigators have posited that nest predation risk may be especially high in noisy areas because noise may mask sounds of predators approaching the nest (Warren et al. 2006, Slabbekoorn & Ripmeester 2008, Brumm 2010). In contrast, opportunistic avian and mammalian nest predators may also have a reduced ability to detect nests in noisy areas, which could result in lower predation risk with increases in noise exposure. Because nest predation is often the primary cause of nest failure for many birds (Ricklefs 1969, Wilcove 1985, Martin 1993, Haskell 1995) and is an

important force influencing long-term local population viability (Sherry & Holmes 1992), it is critical to understand whether nests in the increasing number of noisy habitats have altered predation risk due to the presence of anthropogenic noise.

Contrary to conservation concerns that noise may decrease nesting success, we recently found nest predation decreased with increased background noise amplitudes for the avian community as a whole and for individual species nesting within piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands (Francis et al. 2009). This finding suggests that nest predators may also be negatively affected by noise, but this effect could reflect differences in predator behavior in noisy areas compared to quiet areas (functional responses), or a difference in the relative abundance of predators in noisy areas compared to quiet areas (numerical response; Chalfoun et al. 2002). For functional responses, noise may negatively affect predators' abilities to locate nests in two ways: (1) acoustic masking of cues used to located nests or (2) increased vigilance through perceived predation risk (Quinn et al. 2006). In contrast, noise may cause a numerical response by predators through a decrease in nest predator abundances in noisy areas.

Predators are known to use activity near the nest to locate prey nests (e.g., Martin 1993, Martin & Ghalambor 1999, Martin et al. 2000, Fontaine et al. 2007), and acoustic cues may play a role in drawing predator attention to activity at or near the nest, such as nestling begging calls (Haskell 1994) and vocalizations from the parents (Major & Kendal 1996). Noise may mask these acoustic cues and interfere with predators' abilities to locate nests, resulting in higher nest success in noisy areas. In

effect, the functional predator response of a reduced ability to detect activity at or near the nest due to noise could have a similar positive effect on nest survival as would a numerical response, in which lower abundances of nest predators in noisy areas result in higher nest success. A numerical decrease in predators within noisy areas may occur for a variety of reasons, including, but probably not limited to, the perception that noise represents danger or predation risk, noise disrupts foraging abilities (Quinn et al. 2006, Schaub et al. 2008), or noise interferes with communication among conspecifics (Slabbekoorn & Ripmeester 2008, Brumm 2010). Assessments of the influence of the functional and numerical alternatives in explaining patterns of nest predation in noisy areas are lacking. Here, we tested for differences in nest predation patterns in quiet and noisy habitats by using artificial nests, which separate the influence of activity at the nest on predation risk.

Artificial nests lack parent and nestling activity; therefore, predation outcomes from artificial nests are independent of activity at the nest that can influence predation risk (Fontaine 2007) and can provide insight on the relative contributions of functional and numerical predator responses on nest predation risk. If artificial nest predation was higher on quiet control sites than noisy treatment sites, as was observed with real nests (Francis et al. 2009), it may be indicative of a numerical predator response, a reduction in the abundance of important nest predators. In contrast, if artificial nest predation rates were equivalent or higher on noisy treatment sites than quiet control sites, unlike that of real nests, it may be indicative of a functional predator response to noise. That is, nest predators may exist in noisy areas but experience a reduced ability to locate real nests

due to effects of noise. It is important to note that numerical and functional predator responses are not mutually exclusive; higher artificial nest predation on control sites would be indicative of a numerical response, but does not exclude the possibility that a functional response may also contribute to the pattern of increased nest success in noisy habitat. Thus, in this study we (1) examine the effects of the presence and intensity of gas well compressor noise and nest site habitat variables on survival of artificial nests, (2) compare predation rates of artificial nests with those of real nests reported in Francis et al. (2009), and (3) identify predators of artificial nests in the piñon-juniper woodland community with artificial nests paired with motion-triggered cameras.

METHODS

In 2006 and 2007, we conducted artificial nest experiments at the Rattlesnake Canyon Habitat Management Area (RCHMA), which is managed by the Farmington Field Office of the Bureau of Land Management (BLM), San Juan County, New Mexico. This area is dominated by piñon-juniper woodlands and open big sagebrush (*Artemisia tridentata*)-grasslands. RCHMA, like other regions of the San Juan Basin in Colorado and New Mexico, is an extensively developed energy producing area. In 2003, the San Juan Basin had approximately 18,000 active oil and gas wells (BLM 2003) and well density has increased markedly since that time (C. D. Francis, pers. obs.).

Throughout RCHMA, gas wells are often coupled with compressors, which generate noise levels that are hazardous to humans (Habib et al. 2007, OSHA 2009). These compressors aid in the transportation of gas through pipelines and run 24 hours a day, 365 days a year aside from periodic maintenance. Because noisy compressors in

RCHMA are present on some well pads (treatment sites) and absent on others (control sites), the area provides a unique opportunity to determine the influence of noise on natural populations and communities. At our study sites, human activity and vegetation does not differ on or around well pads with and without noisy compressors; thus, effects of noise are separated from other confounding variables. Further details regarding habitat similarities on treatment and control site can be found in Chapter II and Francis et al. (2009).

We placed artificial nests on treatment and control sites in May 2006 and 2007. In ArcGIS, we drew two concentric circles around gas well pads – one at 50 m from the study site center (compressor exhaust pipe for treatment sites or gas well head for controls) and one at 150 m. We selected 50 m to avoid the well pad itself and 150 m to ensure for significantly higher noise amplitudes on treatment sites compared to control sites. Within these concentric circles, we generated 25 random artificial nest points. In 2006, we used two treatment sites and two control sites with 25 nests per site, for a total of 100 nests. In 2007, we used three treatment sites and three control sites, each with 25 nests for a total of 150 nests.

Using a hand-held Global Positioning System (GPS) unit, we located each artificial nest point and wired a nest approximately 2 m high in the nearest appropriate juniper tree. We placed nests near a branching point from the trunk or in a fork of a main branch with height and position mimicking nest placement by the Gray Flycatcher (*Empidonax wrightii*) in our study area. We mimicked Gray Flycatcher nests because this species is common to our study area and because its typical nest height (≈ 2 m) is

easy to access. Artificial nests were canary nests manufactured with bamboo wicker (Art #B-1980, Rolf C. Hagen Corp.). We covered the inside and outside of the nest with wood excelsior (Western Excelsior, Mancos, CO) to mimic the appearance of Gray Flycatcher nests, which are constructed with shredded juniper bark in our study area (Sterling 1999, C.D. Francis, pers. obs.). The mean outer diameter of the canary nests was 10.0 ± 04 cm (n = 15) and with the wood excelsior covering was within the reported diameter range of real Gray Flycatcher nests (outside diameter reported as 12.1 ± 1.43 cm SD in Sterling 1999).

Three Japanese Quail (*Coturnix coturnix*) eggs (obtained from B and D Game Farm, Harrah, OK) were placed in each nest within three days of setting nests in trees. We used quail eggs produced from young hens that were smaller than typical quail eggs; the mean size was 20.1 ± 0.6 mm x 26.2 ± 1.1 mm (n = 20), but still larger than the size of Gray Flycatcher eggs (13.7 mm x 17.7 mm SD) reported by Sterling (1999). We used the smallest quail eggs available because previous research demonstrated that some important predators are unable to break open quail eggs with a mean width of 23.5 mm (Haskell 1995) and average length of 30 mm (Roper 1992). In 2006, we placed eggs in nests on 13 May; in 2007, we placed eggs in nests on 22 May. Although leaving human scent on eggs may not affect predation or abandonment of American Robin (*Turdus migratorius*) nests (Ortega et al. 1997), we wore latex gloves while handing nests and eggs to reduce potential effects of human scent (Whelan et al. 1994). In 2006, we checked the contents of each nest every five days for a total of 15 days (three nest visits). In 2007, we checked the contents of each nest every four days for a total of

12 days (three nest visits). Accordingly, nests on control and experimental sites were visited with the same frequency.

In 2006, we recorded nest height, nest tree diameter at breast height (DBH), and distances to the nearest tree, snag, and study plot center (distance to well head on control sites and distance to compressor exhaust pipe on treatment sites). We also measured sound pressure levels (SPL) using A- and C-weighted amplitude measurements for 30 seconds on three separate days and times at each artificial nest to control for the effects of atmospheric variability on sound propagation from the compressors. We measured SPL with Casella® convertible sound dosimeter/sound pressure meters (model CEL 320 and CEL 1002 converter) that were certified with National Institute of Standards and Technology (NIST) traceable certification. We used 95 mm acoustical windscreens, and we did not take SPL measurements when wind conditions were category three or above on the Beaufort Wind Scale (≈ 13-18 km/h). Compressor noise contains considerable energy as high as 5 kHz, but had most acoustic energy at very low frequencies (see Fig. 4 in Chapter II). For this reason, we used A-weighted SPL values (dB(A)) because A-weighting filters much of the low frequency compressor noise (< 0.5 kHz) that most birds hear poorly (Dooling & Popper 2007).

In 2007, at each nest we measured SPL as in 2006, but due to the lack of or small effect of other variables on nest success (see Results), we measured only the distance of each nest to the study site center. To document diurnal predator identity on treatment and control sites, we placed 10 motion-triggered digital cameras (Wildview®

Xtreme II) on treatment nests and 10 on control nests. We mounted each camera on a branch in an adjacent tree. When an appropriate adjacent tree was unavailable, the camera was mounted in the nest tree. All cameras were within 1—3 m from nests. We positioned the camera to get a clear view of the nest, but we also attempted to position the camera in a low and relatively inconspicuous location to avoid drawing additional attention to the nest. Artificial nests paired with cameras were selected randomly at each site with three cameras on two treatment and two control sites and four cameras at one treatment and one control site.

ANALYSIS

To determine whether noise exposure influenced artificial nest success, we used generalized linear mixed-models (GLMMs) with binomial errors, where removal or damage to any of the eggs during exposure was considered to be nest failure (0) and no damage or removal of eggs was treated as nest success (1). We treated year as a random effect to account for yearly variation in predation risk and different exposure lengths between years and site as a random effect to account for the fact that nests located at each site were not entirely independent. Nest presence on a treatment or a control site (site-type), SPL and distance to the site center were all treated as fixed effects.

To make comparisons with real nests, and to evaluate the influence of additional predictor variables on nest success, we modeled daily nest survival (DNS) using the

logistic-exposure method (Rotella et al. 2004; Shaffer 2004). This method employs a modified logit-link function to account for the number of days a nest was observed. Each interval between a nest check was used as a single observation. The method we employed used generalized linear models (GLMs) and did not account for the nested nature of our study design, but we view it as a valuable complement to the GLMM analyses that does account for this design in the model structure. Because predictor variables under consideration differed between years, we treated nests from 2006 and 2007 separately to estimate DNS. In 2006, we examined the influence of the following variables on DNS: nest location on site-type (treatment vs. control site), SPL, measured on the A-scale, nest height, DBH, and distances to the nearest tree, snag, and study site center. In 2007, we examined the influence of nest location on site-type (treatment vs. control site), SPL, presence of camera with a nest, and distance to study site center. Predictions of the expected effect on nest success and DNS for each variable are provided in Table 3.1.

For all analyses we used an information-theoretic approach to evaluate support for competing candidate models (Burnham & Anderson 2002) with Akaike's Information Criterion corrected for small sample sizes (AIC_c). We ranked models based on differences in AIC_c scores (ΔAIC_c). For DNS models, we calculated AIC_c scores using the number of known nest survival days, plus all intervals between nest observations ending in nest failure as the effective sample size (N_{eff}; Rotella et al. 2004). Models with ΔAIC_c scores within two of the best models were considered to have strong support and were assigned Akaike weights (w_i) to quantify the degree of support for each. We used

all candidate models with Akaike weights to calculate model-averaged variable coefficients and unconditional 95% confidence intervals (95% CIs). We calculated odds ratios for the model-averaged coefficients and 95% CIs, and we concluded that there was little evidence for the effect of a predictor variable on nest survival or DNS when the odds ratios of the 95% CIs overlapped 1.0. We also weighted the evidence of importance of each variable (relative variable importance) included in candidate models with Akaike weights following Burnham & Anderson (2002). All means are reported ± SE unless otherwise indicated.

Table 3.1 Variables included in GLMM nest survival model & DNS models for artificial nests on treatment and control sites. Predicted effect direction provided for each.

Variable	Abbreviation	Direction of predicted effect
2006-2007 Mixed-effect & DNS Models		
Nest located on a treatment or control site	Site-type	+
Distance of nest to study site center	Dist	–
Sound pressure level at nest, dB(A)	SPL	+
2006 DNS Models Only		
Nest substrate diameter at breast height	DBH	+
Nest height	Nht	–
Distance to nearest snag	Dsnag	–
Distance to nearest live tree	Dtree	–
2007 DNS Models Only		
Camera Presence	CamY	+ / –

RESULTS

Mean SPL values at artificial nests were significantly different on treatment (50.2 ± 0.5 dB(A) and control sites (37.6 ± 0.5 dB(A), $t = 18.32$, $df = 248$, $p < 0.001$) and ranged from 31.3 – 47.4 dB(A) on control sites and 41.2 – 61.2 dB(A) on treatment sites. Means and ranges for other predictor variables are provided in Table 3.2. From the model selection procedure of GLMMs including the random effects of year and site, the top model for nest success included distance to the site center and SPL as fixed effects (Table 3.3). However, two other models also received strong support ($\Delta AIC_c < 2$); one with distance to the site center, SPL and site (treatment/control) and one with SPL as the only fixed factor. Based on the Hosmer-Lemeshow goodness-of-fit test, the top model fit the data ($\chi^2 = 7.62$, $p = 0.47$). Of the model-averaged coefficients from the models with strong support, only SPL had a strong effect on nest success (odds ratio for the 95% CI did not overlap 1.0; Table 3.4). SPL had a positive influence on nest success (Fig. 3.1), supporting the results observed in natural nests (Francis et al. 2009).

DNS models

In 2006, the 100 artificial nests had an effective sample size of 806, and the 150 artificial nests used in 2007 had an effective sample size of 1482. The top DNS model for 2006 contained nest location on treatment or control sites (site-type) and substrate DBH predictor variables and the model fit the data (Hosmer-Lemeshow goodness-of-fit test, $\chi^2 = 4.96$, $p = 0.76$). However, there was also strong support ($\Delta AIC_c < 2$) for four other models, which contained the two variables in the top model, but also distance to

nearest snag, distance to the site center, or SPL (Table 3.5). For 2007, nest location on treatment or control sites was also in the top model with distance to site center, camera presence, and SPL. Two additional models also had strong support (Table 3.5). Our top model for 2007 also fit the data (Hosmer-Lemeshow goodness-of-fit test, $\chi^2 = 4.16$, $p = 0.84$).

Table 3.2 Descriptive statistics for continuous variables used in mixed-effect nest survival and DNS models. Mean ± SE presented, plus range (minimum to maximum).

Variable[a]	**mean ± SE**	**Range**
2006-2007 Mixed-effect & DNS Models		
SPL	43.9 ± 0.5 dB(A)	31.3 – 61.2 dB(A)
Dist	92.6 ± 1.3 m	51.3 – 146.1 m
2006 DNS Models		
DBH	35.7 ± 1.1 cm	6.3 - 92.3 cm
Nht	1.5 ± 0.0 m	0.9 - 2.1 m
Dsnag	6.8 ± 0.4 m	0.3 - 30.0 m
Dtree	2.4 ± 0.2 m	0.2 ± 9.5 m

[a] Abbreviations of variables in Table 1.

Table 3.3 All mixed-effect models, plus null based on 250 artificial nests. *K* is the number of parameters in the model, AIC_c is Akaike's Information criteria for small sample size, ΔAIC_c is the difference in AIC_c values from the top ranking model, and w_i is the Akaike weight, calculated for all models with substantial support ($\Delta AIC_c < 2$). All models contained year and site as random effects.

Model[a]	***K***	**AIC_c**	**ΔAIC_c**	**w_i**
Dist, SPL	5	301.80	0.00	0.53
Dist, SPL, Site-type	6	303.36	1.56	0.24
SPL	4	303.41	1.61	0.23
SPL, Site-type	5	304.87	3.07	
Dist, Site-type	5	305.03	3.23	
Site-type	4	306.30	4.50	
Dist	4	306.45	4.65	
Null - random effects only	3	307.11	5.31	

[a] Abbreviations of variables in Table 3.1.

Table 3.4 Mixed effect model-averaged effect sizes ± SE, odds ratios with 95% confidence intervals and relative variable importance for all variables present in supported models ($\Delta AIC_c < 2$). Bold denotes variables considered to have a strong effect.

Variable[a]	Effect size and direction	Odds ratio	95% CI	Relative variable importance
Dist	-0.01 ± 0.01	0.99	0.97 - 1.01	0.77
SPL	**0.11 ± 0.05**	**1.12**	**1.01 - 1.23**	**1.00**
Site-typeT[b]	-0.20 ± 0.44	0.82	0.35 - 1.93	0.24

[a] Abbreviations of variables in Table 3.1.
[b] Nest presence on a treatment site.

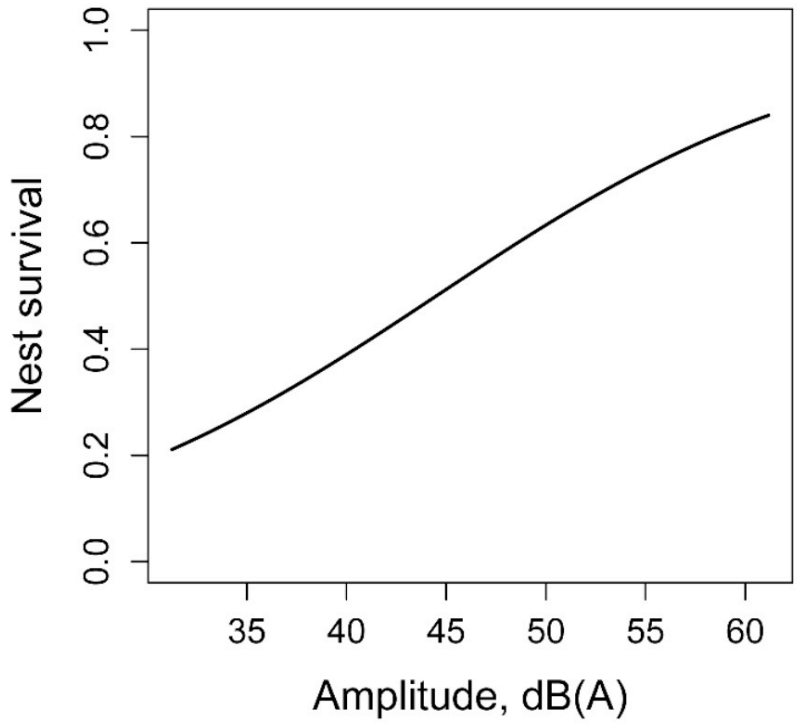


Figure 3.1 Nest survival estimates for nests in both years increased with noise exposure (increased SPL). Estimates are based on model-averaged coefficients from all GLMMs with strong support ($\Delta AIC_c < 2$).

Table 3.5 All DNS models with $\Delta AIC_c < 4$, plus nulls based on 100 artificial nests with an effective sample size of 806 in 2006 and 150 artificial nests in 2007 with an effective sample size of 1482. *K* is the number of parameters in the model, AIC_c is Akaike's Information criteria for small sample size, ΔAIC_c is the difference in AIC_c values from the top ranking model, and w_i is the Akaike weight, calculated for all models with substantial support ($\Delta AIC_c < 2$).

Model[a]	***K***	**AIC_c**	**ΔAIC_c**	**w_i**
2006				
DBH, Site-type	3	255.60	0.00	0.32
DBH, Site-type, SPL	4	256.53	0.93	0.20
DBH, Dsnag, Site-type	4	256.64	1.04	0.19
DBH, Dist, Site-type	4	256.98	1.38	0.16
DBH, Dsnag, Site-type, SPL	5	257.49	1.89	0.13
DBH, Nht, Site-type	4	257.68	2.08	
DBH, Dtree, Site-type	4	257.68	2.08	
DBH, Dist, Dsnag, Site-type	5	258.16	2.56	
DBH, Dist, Site-type, SPL	5	258.46	2.86	
DBH, Dtree, Site-type, SPL	5	258.60	3.00	
DBH, Nht, Site-type, SPL	5	258.62	3.02	
DBH, Dsnag, Nht, Site-type	5	258.72	3.12	
DBH, Dsnag, Dtree, Site-type	5	258.74	3.14	
DBH, Dist, Dtree, Site-type	5	259.03	3.43	
DBH, Dist, Nht, Site-type	5	259.08	3.48	

Table 3.5 Continued

Model[a]	*K*	AIC_c	ΔAIC_c	w_i
DBH, Dist, Dsnag, Site-type, SPL	6	259.52	3.92	
DBH, Dsnag, Dtree, Site-type, SPL	6	259.54	3.94	
Null	1	264.80	9.20	
2007				
Camera, Dist, Site-type, SPL	5	270.70	0.00	0.49
Dist, Site-type, SPL	4	271.60	0.90	0.31
Camera, Site-type, SPL	4	272.41	1.71	0.21
Site-type, SPL	3	272.87	2.17	
Camera, Dist, SPL	4	274.39	3.69	
Null	1	288.70	18.00	

[a] Abbreviations of variables in Table 3.1.

Of the model-averaged variable coefficients, DNS was positively influenced by nest presence on a treatment site in 2006 ($\beta_{Treatment} = 1.04 \pm 0.44$) and SPL in 2007 ($\beta_{SPL} = 0.32 \pm 0.11$, Table 3.6). In 2006, DBH of the nest substrate had small, but strong negative effect on nest success ($\beta_{DBH} = -0.02 \pm 0.01$). Odds of DNS were 2.41 (95% CI: 1.27-4.57) times greater for nests on treatment sites than control sites in 2006. In 2007, odds of DNS were 1.38 (95% CI: 1.11-1.73) times greater for a one dB(A) increase in SPL. The effect sizes for all other model-averaged variable coefficients were

minimal, and because odds ratios for the 95% CIs overlapped 1.0 for each, there was little evidence for the influence of these variables on DNS in either year (Table 3.6).

For 2006, our estimate of DNS based on model-averaged coefficients was 0.75 ± 0.04 (95% CI: 0.69-0.85) on treatment sites and 0.58 ± 0.05 (95% CI: 0.47-0.67) on control sites. In 2007, DNS ranged from 0.21 at low SPL values to over 0.99 at SPL values of 47 dB(A) and above (Fig. 3.2). These DNS estimates were lower than estimated for real nests (treatment sites, 0.99, 95% CI: 0.98-0.99; control sites, 0.97, 95% CI: 0.97-0.98; Francis et al. 2009).

Cameras and nest predators

The cameras photographed predators at six of 11 depredated artificial nests with cameras. Camera flashes were turned off during this experiment; therefore, it is probable that some of the undocumented predation events occurred at night. Additionally, at least one camera on a control site failed to document a predation event due to low batteries. Of the artificial nests with cameras, eight of 10 on control sites were preyed upon, and only three of 10 on treatment sites were preyed upon. Western Scrub-jays (*Aphelocoma californica*) accounted for four of the six photographed predation events, with one on a treatment site and three on control sites. We also documented a least chipmunk (*Tamias minimus*) and a Steller's Jay (*Cyanocitta stelleri*) depredating artificial nests at a treatment site and a control site, respectively.

Table 3.6 DNS model-averaged effect sizes, odds ratios with 95% confidence intervals and relative variable importance for all variables present in supported models ($\Delta AIC_c <$ 2). Bold denotes variables considered to have a strong effect.

Variable[a]	Effect size and direction	Odds ratio	95% CI	Relative variable importance
2006				
DBH	**-0.02 ± 0.01**	**0.98**	**0.96 - 0.99**	**1.00**
Dist	0.00 ± 0.00	1.00	1.00 - 1.00	0.16
SPL	-0.02 ± 0.03	0.98	0.92 - 1.05	0.33
Dsnag	-0.01 ± 0.01	0.99	0.97 - 1.02	0.32
Site-typeT[b]	**0.88 ± 0.33**	**2.41**	**1.27 - 4.57**	**1.00**
2007				
CameraY	-0.45 ± 0.43	0.64	0.28 - 1.48	0.69
Dist	-0.01 ± 0.01	0.99	0.97 - 1.01	0.79
SPL	**0.32 ± 0.11**	**1.38**	**1.11 - 1.73**	**1.00**
Site-typeT[b]	-3.41 ± 2.44	0.03	0.00 - 3.94	1.00

[a] Abbreviations of variables in Table 3.1.

[b] Nest presence on a treatment site.

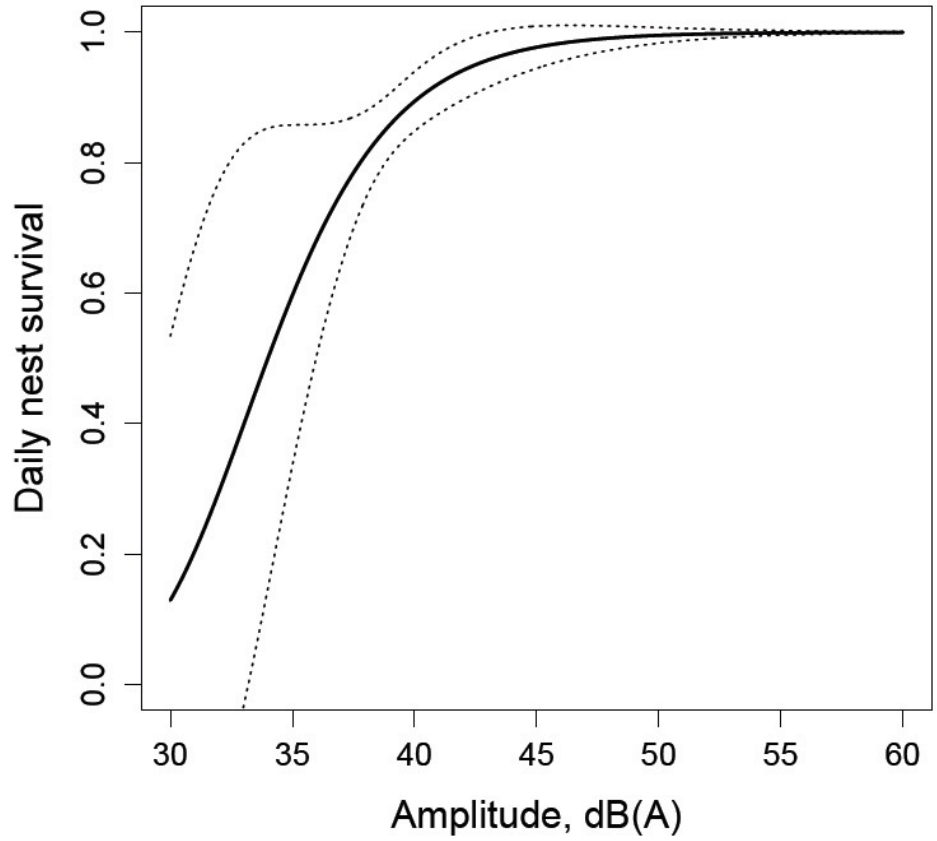


Figure 3.2 SPL positively influenced DNS estimates for artificial nests in 2007. Estimates were based on model-averaged parameter estimates from all DNS models with strong support ($\Delta AIC_c < 2$). Dashed lines denote 95% CI bounds.

DISCUSSION

Our understanding of the mechanistic causes for predation patterns can be confounded in human-altered habitats by numerous ecological factors and potentially disparate responses by predators and prey to individual factors that comprise multi-dimensional human disturbance, such as anthropogenic noise. Here we isolated industrial noise from

other factors common to human disturbance to determine whether lower nest predation in noisy areas was due to lower predator abundances (numerical response) or due to reduced hunting efficiency (functional response) in noisy areas using an experimental approach that evaluated predation risk independent of activity at the nest.

Results from our mixed-model approach demonstrate that artificial nest success increases with SPL, consistent with results from natural nests (Francis et al. 2009). DNS results for each year also support this finding. Because nests lacking activity at the nest did not result in equivalent nest predation rates on treatment and control sites, these results suggest that predators may have lower abundances in noisy regions of our study area and provide evidence for a numerical predator response. We did not find strong support for a functional predator response through a decrease in hunting efficiency due to the effects of noise; however, we cannot conclude that a numerical response is not coupled with a functional response. Of course, it is also possible that reduced foraging efficiency (i.e., a functional response) may be among the many potential mechanisms that cause predators to abandon noisy areas. For example, laboratory work has shown that the greater mouse-eared bat (*Myotis myotis*) avoids foraging in noisy areas. This gleaning bat relies upon prey-generated sounds when foraging and acoustic masking of prey-generated sounds may reduce foraging efficiency (Schaub et al. 2008). It may also be possible that a numerical reduction in predators with increased noise exposure may be due to reduced number of prey. However, we know from our previous work that the density of bird nests does not differ between treatment and control sites, though the composition of nesting species does (Francis et al. 2009). Because scrub-jays and

other opportunistic predators prey upon nest contents from a variety of species, this change in composition is unlikely to cause a numerical reduction in nest predators.

Artificial nest studies have been used in many habitat types to identify predation pressures for nesting birds, yet their use does have some drawbacks, including different rates of nest predation than real nests (Storaas 1988, Weidinger 2001, Pärt & Wretenberg 2002, Faaborg 2004, Villard & Pärt 2004). These differences have been attributed to lack of parental activity at the nest and differences in nest placement, nest material, and the size of the eggs used as bait (Buler & Hamilton 2000, Davison & Bollinger 2000). In our study, care was taken to mimic real nests and use eggs with sizes closer to those found in songbird nests. Although our DNS estimates for artificial nests were much lower than DNS estimates for real nests, the pattern of higher predation on control sites compared with treatment sites and the increase in nest success with increased SPL was consistent between artificial and real nests (Francis et al. 2009). DNS estimates were also different for artificial nests between years, with nest presence on a treatment or control site having the strongest effect on nest outcome in 2006 and SPL having the strongest effect in 2007, but artificial nest success was generally lower in 2006 than 2007. We used different sites in 2006 than those in 2007, and we also started the experiment nine calendar days earlier in 2006. Additionally, nests in 2006 were exposed for three more days than nests in 2007. All of these factors could potentially explain the lack of concordance between years because predation pressure is known to change across habitat-types due to local conditions and time of

year (Johnson et al. 1989, Davison & Bollinger 2000, Small et al. 2007) and because increased exposure will increase probability of predation.

Given the variability in artificial nest success between years, but consistently higher predation rates than with real nests, artificial nest success in our area should not be used to estimate fate of real nests, as is the case in many other studies (Butler & Rotella 1998, Ortega et al. 1997, Wilson et al. 1998, Robinson et al. 2005). Even so, our artificial nest experiments provided key insights on the main objectives of this study: (1) confirmation of differences in relative predation pressure between quiet and noisy sites, while simultaneously eliminating the confounding effect of activity at the nest (Fontaine et al. 2007), and (2) providing support for the hypothesis that predators are in lower densities in noisy sites within our study area, though we could not rule out the possibility that a functional response exists too.

Motion-triggered cameras documented Western Scrub-jays preying upon eggs in artificial nests in four of six photographed predation events, and three of these four events were at artificial nests on control sites. This limited sample is consistent with expectations given the pattern of significantly lower scrub-jay occupancy on treatment sites compared to control sites (Francis et al. 2009). However, our cameras paired at nests did not photograph all predation events. We cannot rule out the possibility that some of the cameras failed to trigger during a diurnal predation event, but we believe this to be unlikely for two reasons. First, it is probable that many of the undocumented predation events occurred at night and were not photographed because camera flashes were turned off. Additionally, the same cameras have been used in subsequent seed

removal experiments and have successfully photographed seed predators at over 95% of seed stations where seeds were removed (C.D. Francis, unpubl. data). It is also worth noting that the majority of undocumented predation events at artificial nests paired with cameras occurred on control sites; four undocumented events on control sites and only one on a treatment site. This difference suggests that there may be more nocturnal predators preying upon artificial nests on control sites than treatment sites, but additional efforts to identify these predators are needed.

We also documented a least chipmunk preying upon one nest. Previous studies have suggested that smaller nest predators, such as chipmunks, are too small to destroy quail eggs commonly used as bait in artificial nest experiments (Roper 1992, Haskell 1995, DeGraaf & Maier 1996, Buler & Hamilton 2000). Our documentation of a chipmunk successfully preying upon quail eggs likely reflects the small quail eggs used in this experiment. It also suggests that use of small eggs may help improve mimicry of real nests so that predation events are not biased against small predators.

Conservation implications

Our experiments showed inherent differences in nest predation, independent of activity at the nest, existed between noisy and quiet sites in our study area. This suggests that predators may be in lower abundances on treatment sites, as was shown to be the case for Western Scrub-jays (Francis et al. 2009). However, we must stress that this result may differ in other habitats with different assemblages of predator and prey species. Because species' responses to noise can differ, nest predators in other habitats may

not respond negatively to noise, potentially leading to different nest predation patterns, such as higher nest predation in noisy areas. This possibility highlights the continued need for thorough field research at the community-level when attempting to characterize the cumulative effects of anthropogenic noise or other factors that constitute human disturbance. If patterns of lower predation in noisy areas hold across other habitats, individuals and species that tolerate noise may be afforded the luxury of lower predation risk, yet those that do not are not so lucky.

CHAPTER IV

NOISE POLLUTION FILTERS BIRD COMMUNITIES BASED ON VOCAL FREQUENCY AND BODY SIZE

ABSTRACT

Human-generated noise pollution permeates natural habitats worldwide and negatively affects humans and wildlife, yet the mechanisms responsible for adverse effects on wildlife are largely unknown. Here we show that (1) masking of acoustic communication by noise may be a dominant mechanism impacting birds and (2) noise filters avian communities nonrandomly. Smaller birds with higher frequency vocalizations may escape acoustic masking of noise and persist in noise areas, whereas larger birds with low-pitched signals that are readily masked by noise avoid noisy habitats. These results are immediately relevant to the global problem of increases in noise pollution and provide critical insight as to which species may tolerate these novel acoustics and which will be muted by the continued spread of our industrial clamor.

INTRODUCTION

Anthropogenic noise pollution (hereafter “noise”) is a prevalent contaminant that not only negative affects human wellbeing (Babisch 2003; Jarup et al. 2008), but may severely influence wildlife (Barber et al. 2010), such as reducing avian species densities, changing community diversity and disrupting interactions among species

(Bayne et al. 2008; Slabbekoorn & Ripmeester 2008; Francis et al. 2009). Most studies to date have suggested that a likely cause for declines in bird abundances in noisy areas is because noise masks vocal communication (e.g., van der Zande et al. 1980; Reijnen et al. 1995), and birds with low frequency vocalizations that are readily masked by low frequency industrial noise may be most strongly affected (henceforth "acoustic masking hypothesis", Rheindt 2003, Slabbekoorn & Peet 2003; Patricelli & Blickley 2006). However, studies have not adequately linked bird declines with underlying mechanistic causes (Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008), primarily because several other mechanisms could explain the declines, such as confounding noise exposure with edge habitat, vehicular motion and lights, direct mortality of birds due to collisions with vehicles, or the masking effect of noise, which impairs an observer's ability to detect birds (Pacifici et al. 2008).

The strongest evidence for an association between acoustic masking of communication and declines in bird densities and community diversity would come from a community-level study adopting a number of critical controls. First, isolating noise as a single variable of interest is essential because it allows one to control for the many confounding stimuli that hinder interpretation of studies using road or urban noise (edge effects, changes in vegetation, visual stimuli of moving traffic, etc.). Second, noise can severely hamper human observers' ability to locate birds (Pacifici et al. 2008); therefore, the ability to eliminate the influence of noise on bird detections is necessary. Finally, because avian vocalizations may vary in time (Luther & Baptista 2010), space (Kroodsma 2004), or in response to vegetation densities (Ryan & Brenowitz 1985) and

noise (Slabbekoorn & Peet 2003; Brumm & Slabbekoorn 2005; Nemeth & Brumm 2009), it is also critical to measure bird vocalizations from individuals in quiet and noisy locations in the same area as measures of habitat use.

RESULTS & DISCUSSION

Here, we report on how acoustic masking of communication filters avian communities using a study system that separates the influence of noise from the influence of other factors that have complicated previous studies (Francis et al. 2009). Our sites were located in woodland habitat adjacent to gas wells with noise producing compressors (noisy treatment sites) and gas wells without compressors (quiet control sites) in NW New Mexico. Typical to most anthropogenic noise, compressor noise at our sites has most energy at low frequencies, though some energy extends beyond 5.0 kHz and represents considerable masking potential for vocalizations of birds in this study (Figure 4.1). Human activity and vegetation did not differ around gas wells with and without noisy compressors (Francis et al. 2009), leaving the presence of compressor noise as the single variable that differed between treatment and control sites. On treatment and control sites we systematically searched for and monitored bird nests for three breeding seasons (see Supporting Material section; Francis et al. 2009) and (ii) conducted point count surveys during one breeding season. Additionally, and perhaps most importantly, because noise reduces observers' abilities to detect birds (e.g., Pacifici 2008), treatment site compressors were turned off during nest searches and bird surveys. We recorded vocalizations from species in the community, taking care to record vocalizations from

individuals located in noisy and quiet areas to capture any potential vocal variation among individuals in quiet and noisy habitat (e.g., Slabbekoorn & Peet 2003; Nemeth & Brumm 2009; Luther & Baptista 2010). From the recordings we extracted several variables describing each species' vocalization frequency, duration and vocalization rate, using a mean of 15.52 ± 2.28 SE individuals per species to calculate the typical song or call for each species (see Supporting Material section).

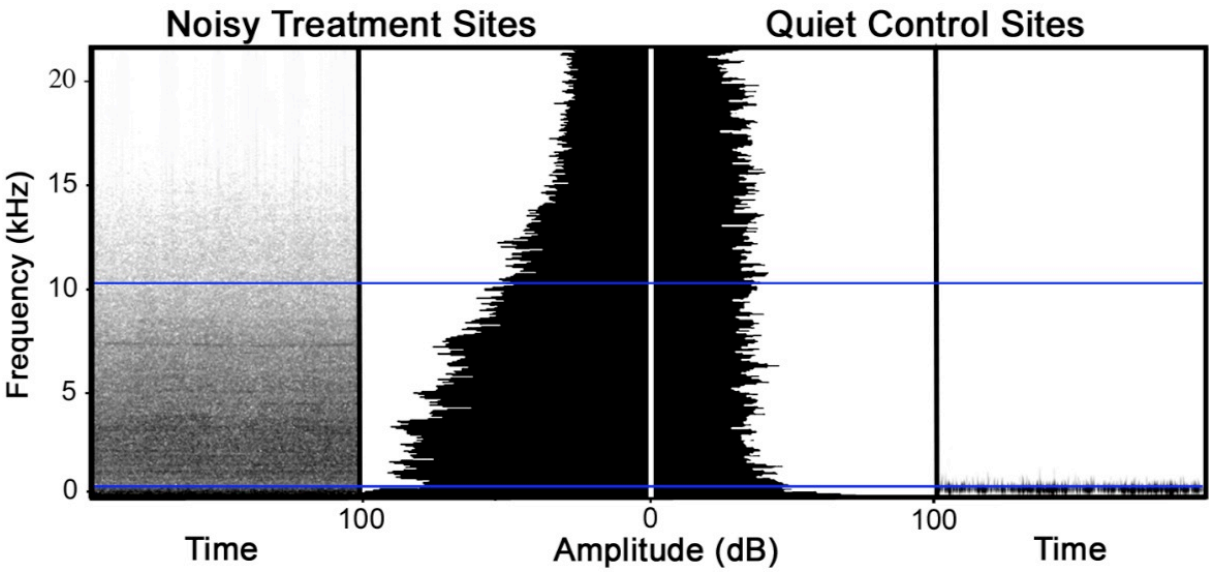


Figure 4.1 Spectrograms (left and right panels) and power spectra (center panels) of typical background noise on a treatment site and on a control site. Darker shades in spectrograms indicate more acoustic energy located at those frequencies, which is reflected by higher amplitude values in the power spectra. On noisy treatment sites compressor noise energy increases at lower frequencies and represents a greater masking potential for species vocalizing at lower pitches. This masking potential is absent on quiet control sites. Blue lines denote approximate minimum and maximum vocal frequencies of birds considered in this study.

To determine whether vocal characteristics influence response to noise in terms of habitat use, we quantified a species' response to noise as: (i) the mean number of nests per site and (ii) mean number of individuals per survey location on treatment and control sites. We evaluated the relative influence of three aspects of vocalizations that may influence acoustic masking, and thus a species' response to noise: frequency, temporal features, and loudness. Following the acoustic masking hypothesis, we expected species with low-pitched vocalizations to suffer most from acoustic masking and thus favor quiet habitat on control sites over noisy habitat on treatment sites. We expected species with short or infrequent signals to be more sensitive to noise and be more common on control sites than treatment sites because their signals have less redundancy than species with long or frequent signals that may be more easily detected by a receiver in noisy habitat (Brumm & Slabbekoorn 2005). In terms of vocalization loudness, we expected species that vocalize softly at low amplitudes to be more susceptible to acoustic masking by noise and more common on control sites than treatment sites than those that vocalize loudly at high amplitudes, which may vocalize "through" background noise. Finally, because avian body size is known to co-vary with vocal features (Ryan & Brenowitz 1985; Tubaro & Mahler 1998; Bertelli & Tubaro 2002), we also included three measures of body size (mass, wingspan and length) as explanatory variables (see Supporting Material section). Due to multicollinearity among measures of body size and vocalization features, we generated two principal components from these measures so that the first principal component (PC1; 47.4% of total variation) was negatively associated with vocalization length and number of notes

and the second principal component (PC2; 31.4% of total variation) was negatively associated with body mass and vocalization rate, but positively associated with five measures of vocalization frequency (see Supporting Material section).

We used generalized linear models (GLMs) to investigate the strength of support for species vocalization loudness (see Supporting Material section; Cardoso 2010), PC1 and PC2 in predicting the two measures of response to noise using an information-theoretic approach with model-averaging to identify the most parsimonious models with the best explanatory power (Burnham & Anderson 2002; Table 4.1). PC2, positively associated with vocal frequency and negatively associated with body mass and vocalization rate, was the only variable with as strong effect on species responses to noise and had a stronger effect on nesting response to noise (β_{PC2} = 0.48 ± 0.12 SE) than the point-count response (β_{PC2} = 0.20 ± 0.09 SE, Figure 4.2). Larger species with lower frequency vocalizations (extending < 2.0 kHz), such as the western tanager (*Piranga ludoviciana*), black-headed grosbeak (*Pheucticus melanocephalus*), and mourning dove (*Zenaida macroura*) had strong negative responses to noise. Smaller species with higher frequency vocalizations (mainly < 3.0 kHz), such as the blue-gray gnatcatcher (*Polioptila caerulea*) and chipping sparrow (*Spizella passerina*), often failed to respond to noise in terms of habitat use, while others, such as the house finch (*Carpodacus mexicanus*), black-chinned hummingbird (*Archilochus alexandri*), and bushtit (*Psaltriparus minimus*), responded positively. To counter the potential influence of multiple species within the same genus or the three non-songbirds (black-chinned hummingbird, mourning dove, hairy woodpecker (*Picoides villosus*)), we also reran the

analyses: once using genera-level patterns (Table 4.2) and once using only songbirds (Passeriformes; Table 4.3). PC2 was always in the top-model and retained a strong effect on response to noise for genera-level patterns (nesting $\beta_{PC2} = 0.51 \pm 0.12$ SE; point-count $\beta_{PC2} = 0.20 \pm 0.08$ SE) and for nesting songbirds ($\beta_{PC2} = 0.38 \pm 0.16$ SE), but not for songbird point-count responses to noise ($\beta_{PC2} = 0.07 \pm 0.11$ SE, Table 4.4).

That two distinct measures of response to noise were both best explained by PC2 provides compelling evidence for a causal relationship between sensitivity to noise due to acoustic masking of low frequency vocal signals and supports the acoustic masking hypothesis. Another study had provided limited evidence for the role of vocal frequency in species' sensitivities to noise (Rheindt 2003), also illustrating that species with low frequency vocalizations appear most sensitive, but the findings were compromised by complications associated road noise, lack of repetition and low statistical power (Slabbekoorn & Ripmeester 2008). Here, we control for these variables and show how vocal frequency, body size and vocalization rate are factors influencing avian habitat use in response to noise.

Table 4.1 Model-selection table with full dataset. All candidate models are shown, including the null (intercept only model). *K* is the number of parameters in the model, AIC*c* values are Akaike's information criteria for small sample size and ΔAIC_c is the difference in AIC*c* values from the top-ranking model. Models with $\Delta AIC_c \leq 2$ are considered to have substantial support and used to calculate Akaike weights (w_i).

Candidate models	***K***	**AIC_c**	**ΔAIC_c**	**w_i**
Nesting Response				
PC2	3	73.55	0.00	0.72
PC2, loudness	4	75.47	1.92	0.28
PC1, PC2	4	76.25	2.71	
PC1, PC2, loudness	5	78.41	4.86	
Loudness	3	85.32	11.78	
Null	2	87.31	13.77	
PC1, loudness	4	88.02	14.47	
PC1	3	89.81	16.27	
Point-count Response				
PC2	3	55.43	0.00	0.73
PC2, loudness	4	57.37	1.94	0.27
PC1, PC2	4	57.96	2.53	
Loudness	3	58.82	3.39	
Null	2	59.31	3.88	
PC1, PC2, loudness	5	60.08	4.65	
PC1, loudness	4	61.28	5.85	
PC1	3	61.67	6.23	

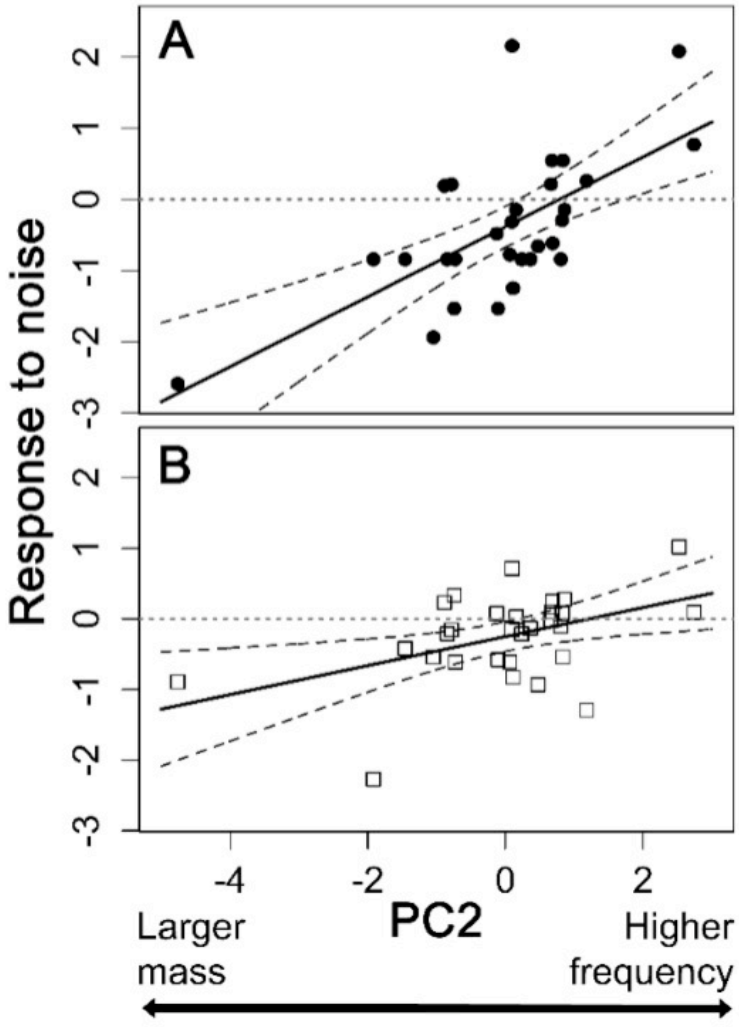


Figure 4.2 PC2 (positively associated with five frequency features and negatively associated with body mass) had a stronger effect on species' (**A**) nesting response to noise than (**B**) point-count response to noise. Y-axis reflects the natural log of the response to noise: (**A**) mean number of nests per treatment vs. control sites and (**B**) mean number of individuals per survey location on treatment vs. control sites. Values above zero (dashed horizontal lines) indicate greater abundance on treatment sites (positive response to noise) and values below zero indicate greater abundance on control sites (negative response to noise). Distance from zero reflects the strength of the response. Solid lines reflect model-averaged estimated effect of PC2 on response to noise and long-dashed lines denote 95% unconditional confidence intervals.

Table 4.2 Model-selection table using species pooled to genera. All candidate models are shown, including the null (intercept only model). *K* is the number of parameters in the model, AIC*c* values are Akaike's information criteria for small sample size and ΔAIC_c is the difference in AIC*c* values from the top-ranking model. Models with $\Delta AIC_c \leq 2$ are considered to have substantial support and used to calculate Akaike weights (w_i).

Candidate models	*K*	AIC_c	ΔAIC_c	w_i
Nesting Response				
PC2	3	69.07	0.00	0.72
PC1, PC2	4	70.98	1.91	0.28
PC2, loudness	4	71.31	2.25	
PC1, PC2, loudness	5	73.40	4.33	
Loudness	3	81.58	12.51	
Null	2	83.19	14.12	
PC1, loudness	4	83.65	14.58	
PC1	3	85.27	16.20	
Point-count Response				
PC2	3	51.95	0.00	0.65
PC1, PC2	4	53.19	1.24	0.35
PC2, loudness	4	54.21	2.26	
Null	2	55.22	3.27	
Loudness	3	55.28	3.33	
PC1, PC2, loudness	5	55.58	3.63	
PC1, loudness	4	56.51	4.56	
PC1	3	56.53	4.59	

Table 4.3 Model-selection table with songbirds only. All candidate models are shown, including the null (intercept only model). *K* is the number of parameters in the model, AIC*c* values are Akaike's information criteria for small sample size and ΛAIC_c is the difference in AIC*c* values from the top-ranking model. Models with $\Lambda AIC_c \leq 2$ are considered to have substantial support and used to calculate Akaike weights (w_i).

Candidate models	***K***	**AIC_c**	**ΛAIC_c**	**w_i**
Nesting Response				
PC2	3	64.54	0.00	1.00
Loudness	3	67.05	2.50	
PC2, loudness	4	67.09	2.55	
PC1, PC2	4	67.35	2.81	
Null	2	67.70	3.15	
PC1, loudness	4	69.81	5.27	
PC1, PC2, loudness	5	70.19	5.65	
PC1	3	70.24	5.70	
Point-count Response				
PC2	3	50.96	0.00	0.38
Null	2	51.04	0.08	0.37
Loudness	3	51.76	0.80	0.26
PC2, loudness	4	53.53	2.57	
PC1	3	53.59	2.65	
PC1, PC2	4	53.69	2.73	
PC1, loudness	4	54.56	3.60	
PC1, PC2, loudness	5	56.56	5.60	

Table 4.4 Model-averaged effect size estimates and standard errors for the influence of explanatory variables on nesting and point-count responses to noise for all variables present in supported models ($\Lambda AIC_c < 2$). Results from analyses with the full dataset, plus reanalysis with songbirds only or at the genus-level are presented. Standard errors (SE) and 95% confidence intervals are all model-averaged unconditional estimates unless otherwise noted. Explanatory variables with strong effects are in bold.

Model-averaged parameters	Effect size ± SE	95% CIs
Full set: Nesting Response		
PC2	**0.479 ± 0.119**	**0.247 - 0.712**
Loudness	-0.056 ± 0.121	-0.292 - 0.181
Full set: Point-count Response		
PC2	**0.197 ± 0.867**	**0.027 - 0.367**
Loudness	-0.040 ± 0.875	-0.212 - 0.131
Songbirds: Nesting Response		
PC2	**0.382 ± 0.157**[1]	**0.074 - 0.690**[1]
Songbirds: Point-count Response		
PC2	0.074 ± 0.112	-0.146 - 0.294
Loudness	-0.061 ± 0.111	-0.279 - 0.157
Genera: Nesting Response		
PC1	0.023 ± 0.049	-0.072 - 0.118
PC2	**0.506 ± 0.115**	**0.280 - 0.732**
Genera: Point-count Response		
PC1	0.028 ± 0.049	-0.068 - 0.123
PC2	**0.195 ± 0.084**	**0.032 - 0.359**

[1]SE and 95% CIs values are not model-averaged estimates. PC2 was only variable in top-models.

Though avian body mass is negatively related to vocalization frequency (Ryan & Brenowitz 1985; Tubaro & Mahler 1998; Bertelli & Tubaro 2002) and can be positively related to vocal loudness (Cardoso 2010), we found loudness not to affect response to noise, but the influence of body mass and frequency were quiet strong. This difference suggests that larger birds' abilities to vocalize at higher amplitudes may not be sufficient to overcome the masking potential of noise, but that the frequency content of the signal is more important. That is, larger birds may be able to vocalize more loudly, but they also vocalize at lower frequencies where noise has more acoustic energy. This distinction suggests that body size may be used as a coarse proxy for predicting species' sensitivities to noise due to its relationship with vocalization frequency, regardless of vocal loudness. Of course, these distinctions should only relate to negative or neutral responses to noise and do not explain why smaller species with higher-pitched vocalizations responded positively to noise despite no differences in major habitat features (Francis et al. 2009). It is likely that these positive responses are related to species' abilities to successfully dispatch critical signals, but also may represent habitat selection based on lower interspecific competition or cues indicative of lower nest predation risk in noisy areas (Francis et al. 2009).

That most (90%) of the negative nesting responses to noise were stronger than the negative point-count responses to noise (Figure 4.2) may represent a greater proportion of unpaired males in noisy habitat relative to quiet habitat. This pattern of lower pairing success by territorial males in noisy habitat relative to quiet habitat was found in ovenbirds (*Seiurus aurocapilla*; Habib et al. 2007) and reed buntings (*Emberiza*

schoeniclus; Gross et al. 2010). In our study area birds were not uniquely marked (i.e., banded or otherwise marked); therefore, we are unable to determine whether more young, subdominant males with less breeding experience may have established territories in noisy areas and failed to attract mates because individual quality is perceived by females to be lower or because males in noisy areas may have more difficulty attracting mates due to acoustic masking of their acoustic signals. Whether due to subdominant males or distorted songs, a large proportion of unpaired males in noisy habitat would also explain why PC2 did not have a strong influence on the subset of point-count data restricted to songbirds. Still, unsuccessful pairings may not explain the difference in the two responses to noise by the two species with the strongest positive nesting responses (black-chinned hummingbird and house finch). These species' especially strong positive nesting responses to noise may be due to reduced interspecific competition and predation risk, as mentioned previously.

Diverse habitats worldwide are now exposed to anthropogenic noise (Barber et al. 2010) and our findings provide compelling support for the acoustic masking hypothesis and strengthen the preponderance of evidence that acoustic masking by noise is a selective force shaping the ecology and evolution of birds in noisy landscapes. Within and among species, birds most likely to suffer from the din in human-altered habitats are those with larger bodies and low frequency signals. In contrast, smaller individuals and species may not only persist in noisy habitats through transmission of higher pitched signals, but benefit from increased reproductive success relative to those nesting in less noisy habitats due to reduced predation risk (Francis et

al. 2009). Given that increases in noise exposure is a global phenomenon, more attention is needed to determine if populations are coping to this novel pressure via adaptive change and whether noise is an agent of ecological extirpation for diverse taxa that rely on acoustic communication.

SUPPORTING MATERIAL

Study Sites

We conducted our study within Rattlesnake Canyon Habitat Management Area (RCHMA), which is located in the San Juan Basin in northwestern New Mexico and managed by the Bureau of Land Management (BLM). RCHMA is dominated by piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands and is within one of the nation's most developed energy-producing regions (over 20,000 active oil and gas wells within the San Juan Basin). Gas wells are often coupled with compressors, which aid in the transportation of gas through pipelines and run 24 hours a day, 365 days a year aside from periodic maintenance and our bird surveys and nest searches (Francis et al. 2009; Chapter II). These compressors generate low frequency noise at amplitude levels that are hazardous to humans (Habib et al. 2007; OSHA 2009). Because noisy compressors are present on some well pads (treatment sites) and absent on others (control sites), RCHMA provides a unique opportunity to determine the influence of noise on natural populations and communities. With the exception of background noise amplitudes, which is significantly higher on treatment sites than control sites through a distance of 400 m from the compressor or wellhead, human activity and vegetation does

not differ on and around well pads with and without noisy compressors that are used in this study (Francis et al. 2009; Chapter II); thus, effects of noise are separated from other confounding variables that complicated attempts to characterize the influence of noise on wildlife.

Nest searches and bird surveys: response to noise data

We searched for and monitored nests at nine treatment and nine control sites during the breeding seasons of 2005 and 2006 and ten treatment and eight control sites in 2007. Methodological details can be found in Francis et al. (2009) and Chapter II. In 2007 we also conducted point count survey at eight control sites and five treatment sites with compressors turned off during our surveys on treatment sites. Within two concentric circles around each well on control sites or compressor on treatment sites (50 m and 150 m), we surveyed 13-16 randomly generated point count stations. Each station was visited twice during the study. At each point count station, we conducted a seven-minute bird survey, and all surveys were completed between 7:00 and 12:00. Because of increases in identification error with large distances, we truncated all observations at 60 m from the point count station, using the closest distance from which each individual was detected.

We estimated the nesting response to noise as the ratio of the mean number of nests per noisy treatment site and quiet control site. Abundance response to noise was estimated as the ratio of the mean number of individuals per survey station on noisy treatment and quiet control sites.

$$y = \log_e\left(\frac{mean\ \ no.\ nests\ or\ individuals\ on\ treatment\ sites\ or\ survey\ stations}{mean\ \ no.\ nests\ or\ individuals\ on\ control\ sites\ or\ survey\ stations}\right)$$

Prior to calculating the mean number of nests per site or individuals per survey station, we performed a quantitative adjustment to the data by adding one to the total number of nests or individuals detected on treatment or control sites. This was necessary because some species were not detected on one of the two site-types, precluding our ability to gauge response to noise as a ratio. Subsequently, this ratio is used as an indication of the relative strength of the response of each species to noise in terms of habitat use.

Species traits: predictor variables

Vocalizations of all species were recorded at sites in our study area between 11 May and 2 July 2009. To ensure for independence of samples, we only sampled one individual per species at each site or, when we did sample more than one individual per species on a site, we only sampled individuals that maintained non-adjacent territories.

We recorded vocalizations using a Marantz PMD 660 Digital recorder using a directional shotgun microphone (Audio-technica AT-815) pointed directly at the vocalizing individual. We recorded vocalizations for entire song or call bouts (i.e. duration that an individual vocalizes from a single perch). All vocalizations were recorded when wind speed was less than category three (≈ 13-18 km/h) on the Beaufort Wind Scale.

For each individual recorded, we randomly selected five strophes or calls from each recording and measured the following variables: vocalization length, number of notes, vocalization rate, minimum and maximum frequency, peak frequency (the frequency vocalized at the highest amplitude), peak frequency of the lowest note (highest amplitude of the call or song's lowest note), and vocalization bandwidth. For all songbirds (order Passeriformes) we measured songs and measured primary calls for all other species and corvids (order Passeriformes, family Corvidae). Peak frequency and peak frequency of the lowest note were measured automatically, and all other measurements were performed manually in RavenPro 1.3 (Charif et al. 2008). We used a sampling rate of 48 kHz and a Hamming window with a fast Fourier transformation (FFT) length set to 1024, providing a spectral resolution of 47 Hz. The spectral variables were averaged for each vocalizing individual to obtain a mean value representing each variable for vocalizations of each male. For two species, the piñon jay (*Gymnorhinus cyanocephalus*) and black-chinned hummingbird (*Archilochus alexandri*), we only recorded a single vocalization for each. Therefore, we used vocalizations archived at the Cornell University Macaulay Library (http://macaulaylibrary.org/index.do) to increase the number of individual samples for these two species using recordings made in western North America. A mean of 15.52 ± 2.28 SE (min = 5, max = 55) individuals were sampled per species to describe a typical species-specific vocalization in our study area.

Loudness scores

Singing or calling loudly may be another mechanism by which species may successfully dispatch signals in noisy environments, and different species may be expected to vocalize at higher amplitudes given their evolutionary history and body size (Ryan & Brenowitz 1985). However, measuring vocal amplitude in free-living birds is often impractical because it requires measuring the signal from directly below a singing individual to control for the directional radiation of soundwaves at a known distance (Brumm 2004). To overcome this problem we followed the methods of Cardoso (2010) to rank vocalization loudness. Four ornithologists with extensive field experience working with birds common to piñon-juniper woodlands independently scored vocalization loudness of breeding birds common to our study area (including 21 species not under consideration here). Each observer scored vocalization loudness on a scale of one to four, with four denoting the loudest. Observers were asked only to score those species for which he or she had considerable experience. We then used the mean score for each species as an index of vocalization loudness.

Morphology

In birds, species vocal features have been shown to co-vary with body size (e.g., Ryan & Brenowitz 1985; Tubaro & Mahler 1998; Bertelli & Tubaro 2002). Therefore, we examined the effects of three measures of body size on response to noise. Body mass, wingspan and body length data were gathered from The Birds of North America and Dunning (2008).

Analyses

As expected from previous research (Ryan & Brenowitz 1985; Tubaro & Mahler 1998; Bertelli & Tubaro 2002), many vocal and morphological features were highly correlated. To enable comparisons across taxa with different responses to noise, and to reduce the number of candidate explanatory variables, we generated two principal components of log-transformed morphological, spectral and temporal measures. The first principal component (PC1) accounted for 47.4% of the total variation among these measures (eigenvalue = 1.66) and the second principal component (PC2) accounted for 31.4% (eigenvalue = 1.35). An increase in PC1 scores was associated with a decrease in vocalization length (-0.69) and number of notes (-0.65). An increase in PC2 scores was associated with a decrease in body mass (-0.55) and song or call rate (-0.30) and an increase in all frequency variables: peak frequency of vocalization (0.30), peak frequency of the lowest note (0.31), lowest frequency (0.29), highest frequency (0.31), and frequency range (0.34). Thus, PC1 reflected variation in vocalization length and PC2 reflected variation in body mass, vocalization rate, and vocal frequency. Loudness scores were not strongly associated with either of the principal components.

We used generalized linear models (GLMs) to investigate the effects of vocalization length and number of notes (represented by PC1), body size and vocal frequency (represented by PC2), and vocal loudness on species' responses to noise as gauged by two separate responses to noise: nesting and point count abundances. Because the original datasets included many distantly related bird taxa, but also two pairs of congeners, we reanalyzed both data sets: once with only passerine birds to

control the potential influence of three non-passerine birds and a second time at the genus level to control for the influence of closely related species.

We used an information-theoretic approach to evaluate support for competing candidate models (Burnham & Anderson 2002) with Akaike's Information Criterion corrected for small sample sizes (AIC_c). We ranked models based on differences in AIC_c scores (ΔAIC_c). Models with ΔAIC_c scores within two of the best models were considered to have strong support. For all candidate models within two ΔAIC_c of the best model, we calculated Akaike weights (w_i) to quantify the degree of support for each. When more than one model had strong support ($\Delta AIC_c < 2$), we used Akaike weights to calculate model-averaged variable coefficients and unconditional standard errors (SE) and 95% confidence intervals (95% CIs). We concluded that there was little evidence for the effect of an explanatory variable on response to noise when the 95% CIs included or overlapped zero. All analyses were completed in program R (R Development Core Team 2009).

CHAPTER V

VOCAL FREQUENCY CHANGE REFLECTS DIFFERENT RESPONSES TO ANTHROPOGENIC NOISE IN TWO SUBOSCINE TYRANT FLYCATCHERS.

ABSTRACT

Anthropogenic noise is prevalent across the globe and may exclude birds from habitats and negatively influence fitness; however, the mechanisms responsible for species responses to noise are not always clear. One effect of noise is a reduction in effective acoustic communication through acoustic masking, yet some urban songbirds compensate for masking effects of noise by altering their songs. Whether this vocal flexibility is responsible for species persistence in noisy areas is unknown. Here, we investigated the influence of noise on habitat use and vocal frequency of two suboscine flycatchers using a natural experiment that isolated effects of noise from confounding stimuli common to urban and roadside habitats. Gray flycatcher (*Empidonax wrightii*) occupancy declined with increased noise, but vocal frequency did not change with changes in noise amplitude. In contrast, ash-throated flycatcher (*Myiarchus cinerascens*) occupancy was uninfluenced by noise, but it vocalized at a higher pitch with increased noise amplitudes. These results suggest that frequency change may be a mechanism for persistence in noisy habitats, but not all species are capable of noise-dependent signal adjustments. The distinctly different flycatcher responses also raise

important questions regarding which species may or may not cope with an increasingly noisy world.

INTRODUCTION

Ecologists and evolutionary biologists have long recognized the role of the physical environment as a selective force in the evolution of vocal communication (e.g. Richards & Wiley 1980; Slabbekoorn & Smith 2002). All environments are also characterized by background sounds, or noise, which can interfere with important acoustic signals. As background noise amplitude increases, it reduces a receiver's ability to detect and discriminate relevant signals from other acoustics (acoustic masking). Many animals have evolved signal characteristics that minimize acoustic masking from sounds within their natural habitats (*reviewed in* Brumm & Slabbekoorn 2005), yet given the rapid and continued spread of human-altered habitats, animals are now faced with new environmental acoustics that influence acoustic communication.

Anthropogenic ambient noise in cities, along roadways and adjacent to industrialized wildlands presents particular challenges for animals that rely on acoustic communication, especially birds. Because anthropogenic noise is louder and often more continuous than sounds in most natural habitats, it presents an evolutionarily novel condition for many species and a potentially important force influencing the ecology and evolution of wild populations (Slabbekoorn & Ripmeester 2008). Noisy habitats also provide a unique opportunity to understand how animals adjust or fail to adjust their acoustic signals to reduce masking effects (Warren et al. 2006).

Several recent studies have shown that species employ a variety of mechanisms to increase the signal-to-noise ratio (SNR) and reduce the masking potential of noise, including spectral, amplitude and temporal adjustments. For example, in the presence of urban noise, several species, including the great tit (*Parus major*, Slabbekoorn & Peet 2003) and reed bunting (*Emberiza schoeniclus*, Gross et al. 2010), increase the minimum frequency of their songs, presumably to "sing-above" low-frequency noise and decrease masking effects. Individual nightingales (*Luscinia megarhynchos*) adjust the amplitude of their songs in response to different intensities of background noise (Lombard effect; Brumm 2004). In terms of temporal adjustments, European robins (*Erithacus rubecula*) inhabiting areas with high levels of anthropogenic noise sing at night, when the acoustic power of background noise amplitudes are an order of magnitude lower (Fuller et al. 2007). Another mechanism by which species may maintain a suitable SNR for signal transmission is through avoidance of noisy areas. Many species may have limited vocal flexibility to reduce the acoustic masking of important signals, potentially explaining patterns of reduced avian densities (Bayne et al. 2008) and reductions in species richness and community diversity in habitats exposed to noise (Francis et al. 2009). These patterns suggest that increased exposure of habitat to noise may represent habitat loss for many species due to unfavorable environmental acoustics for signal transmission, though knowledge of which species are sensitive to noise and which may be more tolerant due to vocal signal change is currently limited.

Amplitude adjustments to increase SNR in noisy environments appear quite common among birds and mammals (*reviewed in* Brumm & Slabbekoorn 2005); however, avian species known to cope with anthropogenic noise with spectral and temporal adjustments are restricted to oscine birds (order Passeriformes, suborder Oscines). There is currently a need to understand whether other avian taxa are capable of those same strategies employed by oscines to overcome the masking potential of noise and settle in noisy habitats, especially among suboscine birds (order Passeriformes, suborder Tyranni), which constitute ~20% of Passeriformes (Sibley & Monroe 1990). Unlike songs of oscine birds, suboscine song appears to develop in the absence of learning (Kroodsma 1984, 2004). Given this distinction, suboscines have typically been thought to have little intraspecific song variation and individuals are expected to have little to no vocal plasticity, yet recent data suggest that previous dogma regarding lack of vocal variation and flexibility may be invalid. For example, intraspecific song variation in suboscines has been recognized as important for individual recognition and discrimination (Kroodsma 2004; Ríos-Chelén et al. 2005). Additionally, ocellated antbirds (*Phaenostictus mcleannani*) change frequency features depending on social interactions (Araya-Ajoy et al. 2009). These examples of song variation among and within individuals may reflect a degree of vocal flexibility that permits individual birds to adjust signals to a variable acoustic environment. However, knowledge of whether suboscines are capable of noise-dependent signal change is currently lacking.

Here we aim to add to the limited understanding of which species can cope with signal interference from anthropogenic noise and which may disappear from the increasing number of habitats exposed to noise. We investigate vocal frequency change and habitat use in response to continuous anthropogenic noise in two suboscine tyrant flycatchers (family Tyranidae): the ash-throated flycatcher (*Myiarchus cinerascens*) and gray flycatcher (*Empidonax wrightii*). In a previous nesting study, we isolated anthropogenic noise from other confounding stimuli often associated with noisy habitat and controlled for habitat differences by using study sites located in habitat adjacent to natural gas wells with and without noisy compressors (Francis et al. 2009). There we found the gray flycatcher to avoid noisy habitat in its nest site selection, yet the ash-throated flycatcher appears uninfluenced by noise in its nest placement (n = 15; Francis, *unpublished data*). Here we use the same natural experiment to further investigate these species' responses to noise in their habitat use. We also test for changes in song and call spectral features in response to noise as potential mechanisms responsible for any differences in habitat use and the observed differences in each species' nest placement with respect to noise. We hypothesize that ash-throated flycatchers are noise tolerant and show no change in occupancy in response to noise amplitude because they modify frequency characteristics of their vocal signals with increases in compressor noise. In contrast, we hypothesize that gray flycatcher occupancy will decrease with increased noise amplitude because they do not adjust frequency characteristics of their vocalizations as noise amplitude increases.

METHODS

Study species

We focused on two flycatchers that breed in open woodlands of western North America. The ash-throated flycatcher is the larger of the two species (≈ 28 g) and is a secondary cavity nester that persists in human-altered habitats (Cardiff & Dittmann 2002). The gray flycatcher is ≈ 12.5 g and is an open cup-nesting species common to piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands (Sterling 1999). Vocalizations of the two species are characterized by different, but overlapping frequencies: gray flycatcher songs and calls are higher pitched (range ≈ 1.5-7.0 kHz) than those of ash-throated flycatchers (range ≈ 1.0-4.0 kHz; Figures 5.1 & 5.2). Given this difference in vocal frequency range, lower frequency ash-throated flycatcher vocalizations are expected to suffer more from acoustic masking and although the strength of acoustic masking by noise may be less severe at higher frequencies, the higher pitched gray flycatcher vocalizations may still be masked by background noise because noise amplitudes at our study sites contain considerable energy as high as 5 kHz (see below; Figures 5.1 & 5.3).

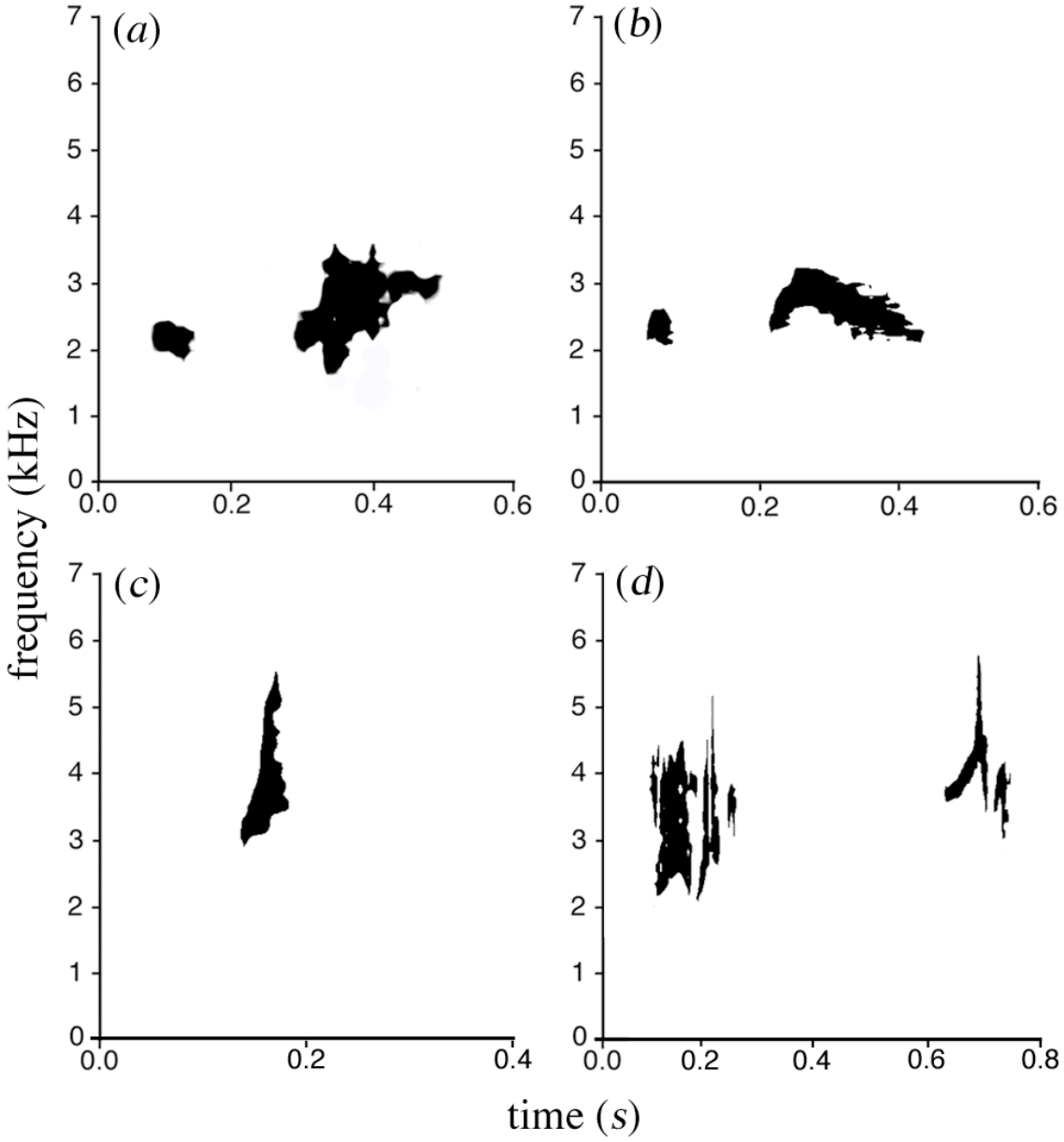


Figure 5.1 Spectrograms of ash-throated flycatcher and gray flycatcher vocalizations. (*a*) Ash-throated flycatcher *ka-brick* call and (*b*) *ha-wheer* song. Gray flycatcher (*c*) *wit* call and (*d*) two part song: the typically sung *chuwip* syllable (first cluster of notes) and the irregularly vocalized *teeap* syllable (second cluster).

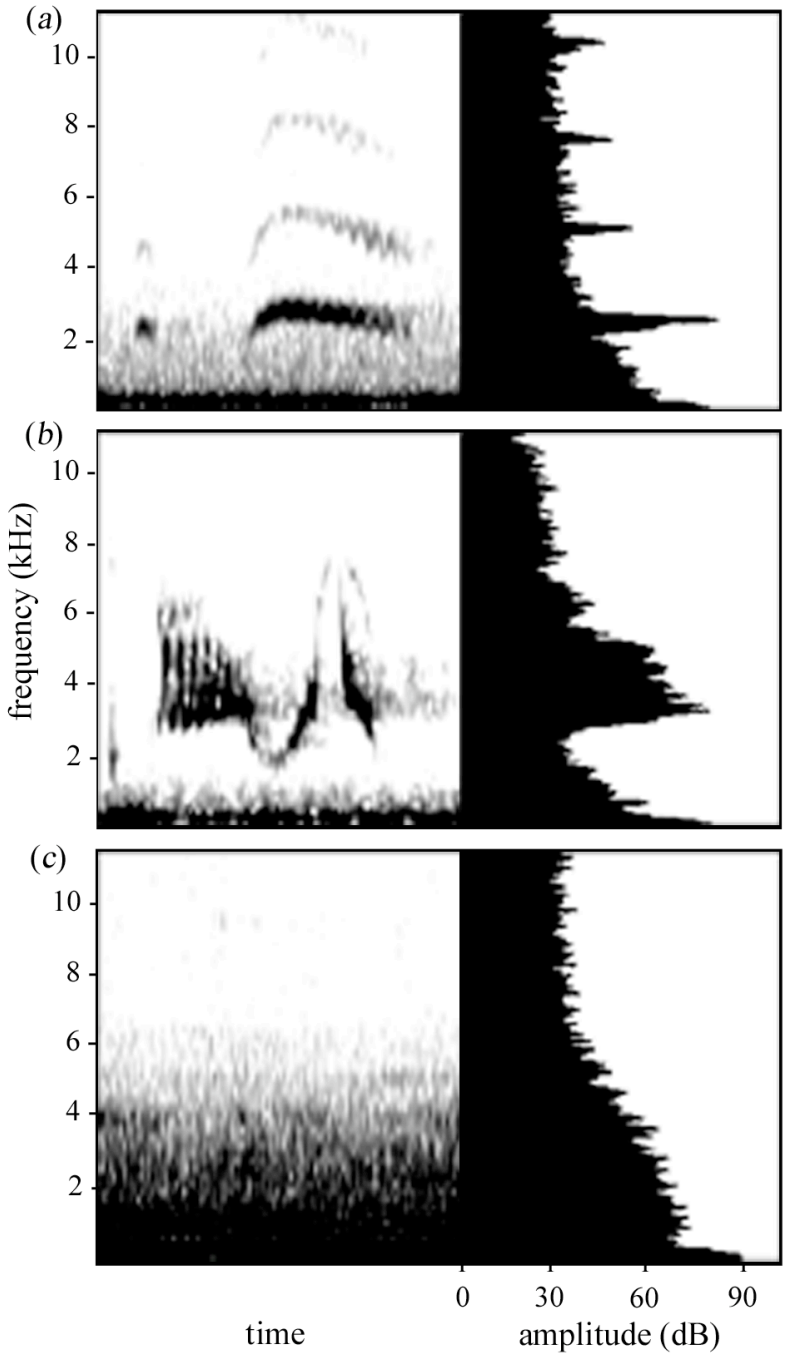


Figure 5.2 Spectrograms (*left*) and power spectra (*right*) of ash-throated (*a*) and gray flycatcher (*b*) songs and of background noise on a treatment site at 200 m from the compressor (*c*). Darker shades in spectrograms indicate more acoustic energy located at those frequencies, which is reflected by higher amplitude values in the power spectra.

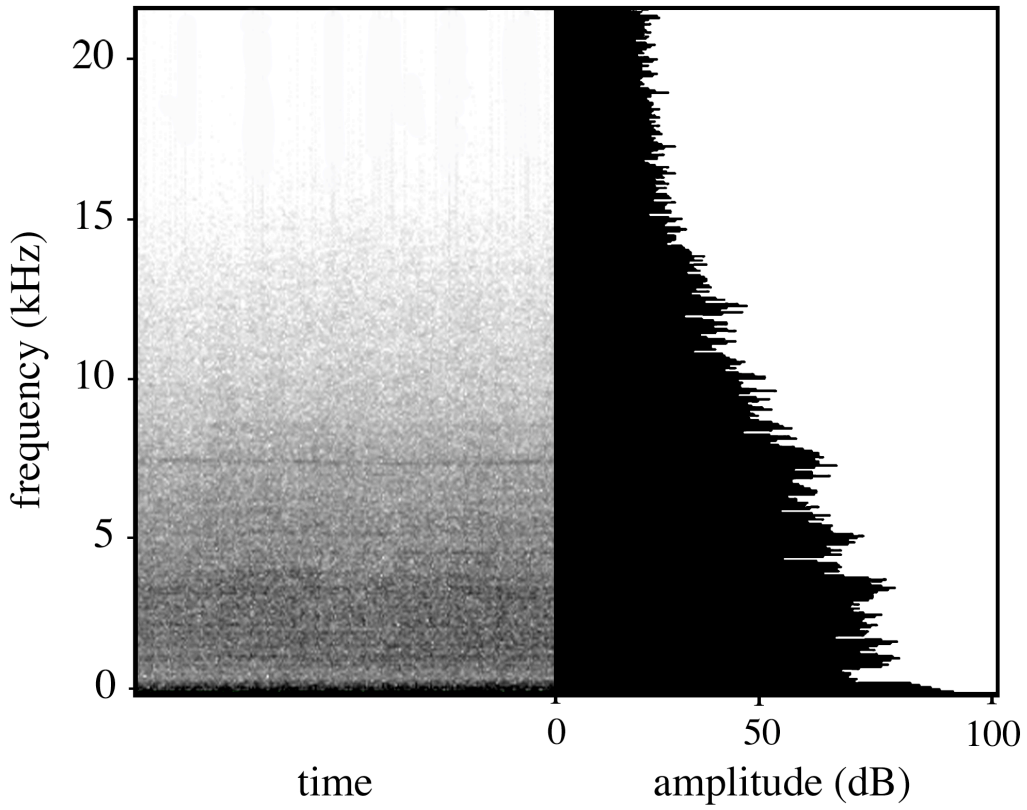


Figure 5.3 Spectrogram (*left*) and power spectrum (*right*) of background noise on a treatment site at 50 m from the compressor. Darker shades in the spectrogram indicate more acoustic energy located at those frequencies, which is reflected by higher amplitude values in the power spectrum. Each illustrate that there is considerable acoustic energy above 5 kHz.

Study area

We conducted our study within Rattlesnake Canyon Habitat Management Area (RCHMA), which is located within the San Juan Basin in northwestern New Mexico, United States of America, and managed by the Bureau of Land Management (BLM). RCHMA is dominated by piñon-juniper woodlands and is within one of the nation's most developed energy-producing regions (BLM 2003). Gas wells are often coupled with compressors, which aid in the transportation of gas through pipelines and run 24 hours

a day, 365 days a year aside from periodic maintenance and our bird surveys and nest searches (Francis *et al.* 2009). These compressors generate noise at amplitude levels that are hazardous to humans (Figures 5.2 & 5.3; Habib et al. 2007; OSHA 2009). Because noisy compressors are present on some well pads (treatment sites) and absent on others (control sites), RCHMA provides a unique opportunity to determine the influence of noise on natural populations and communities. Human activity and vegetation does not differ on and around well pads with and without noisy compressors that are used in this study (Francis et al. 2009); thus, effects of noise are separated from other confounding variables that complicate some other studies.

Point counts

In 2007 we conducted surveys for ash-throated and gray flycatchers in habitat surrounding gas wells at eight control sites and five treatment sites. Within two concentric circles around each well (50 m from the well and 150 m from the well), we surveyed 13-16 randomly generated point count locations. Each point count location was visited twice during the study. At each point count location we conducted a seven-minute bird survey, and all surveys were completed between 7:00 and 12:00. Because of increases in identification error with large distances, we truncated all observations at 50 m from the point count location, using the closest distance from which each individual was detected. Additionally, and perhaps most importantly, treatment site compressors were turned off approximately 20 minutes prior to surveys and remained

off for the duration of surveys to eliminate the negative effect of noise on bird detections (e.g., Pacifici et al. 2008).

Background noise amplitude was measured on the second of two surveys at all control site point count locations. Because compressors were turned off during surveys on treatment sites, we returned to each treatment point count location on a third visit to measure background noise amplitude with the compressors on. Noise amplitude measurements were taken with NIST certified sound pressure meters (Casella® model CEL 320 and CEL 1002 converter) only when there were no birds vocalizing within ≈ 30 m that could bias measurements of the compressor noise and when wind conditions were below category three (≈ 13-18 km/h) on the Beaufort Wind Scale. At each location we measured amplitude with A- and C-weighting, but here we used A-weighted decibels (dB(A)) values in all analyses because A-weighting filters much of the low frequency compressor noise (< 0.5 kHz) that most birds hear poorly (Dooling & Popper 2007) and provides a better representation of acoustic energy at the frequencies at which the two species in this study vocalize (≈ 1.0 – 7.0 kHz, Figures 5.2 & 5.3).

Because there were no systematic differences in habitat characteristics, including, but not limited to canopy cover, tree species and ratios, shrubs, and ground cover, on treatment and control sites, we assumed a constant detection probability on all surveys. Additionally, compressor noise was turned off during surveys on treatment sites as to not bias our ability to locate birds (Francis et al. 2009). To estimate the influence of background noise amplitude on habitat use, we used generalized linear mixed models with the lme4 package in program R (R Development Core Team 2009).

For each flycatcher species, we modeled habitat occupancy using binomial logistic regression with mean background noise amplitude treated as a fixed effect and gas well site as a random effect. We used likelihood-ratio tests to compare models with the fixed effect of mean background noise amplitude to null models containing only the random effect of gas well site. Occurrence at a point count location was defined as whether a species was detected during any of the survey visits.

Vocalization measurements

Ash-throated and gray flycatcher vocalizations were recorded at 37 sites spanning our study area between 11 May and 2 July 2009. Because noise is a permanent feature in our study system that does not vary throughout the day, such as traffic noise, we were able to control for temporal adjustments to vocalizations to overcome masking effects, such as vocalizing during quiet time periods during the day, and focus on frequency characteristics. To ensure for independence of samples, we only sampled one individual per species at each site or, when we did sample more than one individual per species on a site, we only sampled individuals that maintained non-adjacent territories.

We recorded vocalizations using a Marantz PMD 660 Digital recorder using a directional shotgun microphone (Audio-technica AT-815) pointed directly at the vocalizing individual, typically from a distance of 5-15 m. We recorded vocalizations for entire song or call bouts (i.e. duration that an individual vocalizes from a single perch). After recording the song bout, we recorded background noise and measured the amplitude for two minutes from as close to the perch as possible, recording mean and

maximum amplitude values with a sound pressure meter as specified above for point counts. For each individual sampled, we also noted the number of singing males on adjacent territories, distance to the individual, and cardinal direction of the projected vocalization. All measurements and recordings were made when wind speed was less than category three on the Beaufort Wind Scale.

For each individual sampled, we randomly selected five strophes or calls from each recording and measured the following: minimum and maximum frequency, peak frequency (the frequency vocalized at the highest amplitude), peak frequency of the lowest note (highest amplitude of the call or song's lowest note), and vocalization bandwidth (calculated as the minimum frequency subtracted from the maximum frequency). All measurements were performed in RavenPro 1.3 (Charif et al. 2008). We used a sampling rate of 48 kHz and a Hamming window with a fast Fourier transformation (FFT) length set to 1024, providing a spectral resolution of 47 Hz. Vocalization peak frequency and peak frequency of the lowest note were calculated automatically. Measurements of minimum and maximum frequencies were performed manually using cursor measurements at the margin of notes on spectrograms (Slabbekoorn & den Boer-Visser 2006; Gross et al. 2010) with the aid of waveform and power spectrum views to guide precise cursor placement. Despite the overlap with compressor noise, vocalization minimum frequencies were easily distinguished on spectrograms, even from recordings with considerable background noise (Figure 5.4). All spectral variables were averaged for each vocalizing individual so that there was a mean value representing each variable for calls and songs of each male.

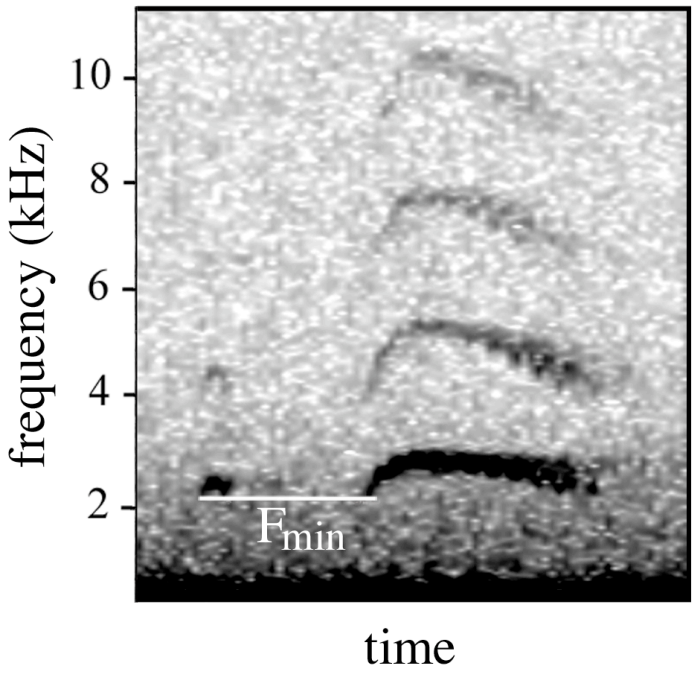


Figure 5.4 Spectrogram of an ash-throated flycatcher *ha-wheer* song at a location in which the mean background noise amplitude was 60.1 dB(A). Vocalization minimum frequency (F_{min}), indicated with the solid white line, was easily identified on spectrograms of recordings at all amplitudes of background noise.

We used linear regression to examine the influence of background noise amplitude on each of the spectral variables for each species' vocalizations. All frequency data were log transformed prior to analyses to stabilize variance and normalize distributions. For each vocalization type (song and call) per species, the significance threshold was adjusted to 0.01 following a Bonferroni correction for multiple comparisons. All analyses were performed in program R (R Development Core Team, 2009).

RESULTS

Noise measurements and species occupancies

Mean point count location amplitudes ranged from 32.1-45.8 dB(A) on control sites and 46.0-68.2 dB(A) on treatment sites. Mean noise amplitude was significantly higher at treatment point count locations (56.1 ± 0.6 SE dB(A)) than on control sites (37.4 ± 0.3 SE dB(A); two sample t-test: two-tailed-$t = 33.309$, df = 195, $p < 0.001$).

Ash-throated flycatchers were detected at 49% of the control (no compressor noise) point count locations ($n = 125$) and 48% of the treatment (compressor noise present, except during surveys) point count locations ($n = 72$). Gray flycatchers were detected at 68% of the control point count locations and 52% of the treatment point count locations. For ash-throated flycatchers, noise amplitude did not influence habitat occupancy estimates (likelihood-ratio test, $\chi^2 = 0.005$, $p = 0.942$). In contrast, background noise amplitude had a significant negative effect on gray flycatcher habitat occupancy (likelihood-ratio test, $\chi^2 = 15.958$, $p < 0.001$). Specifically, gray flycatcher occupancy decreased with respect to increased noise amplitude ($\beta_{amplitude} = -0.125 \pm 0.030$ SE; Figure 5.5).

Noise amplitudes and vocal frequencies

Vocalizing individuals of the two species experienced similar background noise amplitudes. Ash-throated flycatcher vocalizations were recorded within a range of background noise between 37.3-63.6 dB(A). We recorded gray flycatcher vocalizations in background noise amplitudes as low as 35.6 dB(A) and as high as 62.6 dB(A). For

the ash-throated flycatcher, peak frequency of the lowest note for songs and calls, plus call minimum frequency, were all positively related to background noise amplitude (Table 5.1, Figure 5.6). This increase in the call minimum frequency resulted in a significant reduction in call bandwidth with increased background noise amplitude, despite no change in call maximum frequency with respect to noise amplitude (Table 5.1). No other significant relationships between background noise amplitude and spectral characteristics were identified for ash-throated flycatchers (Table 5.1). For gray flycatchers, no song or call spectral characteristics were related to background noise amplitude (all $p > 0.110$; Table 5.2).

DISCUSSION

This study is the first to show a link between noise-dependent habitat occupancy and signal variation in birds and the first to examine changes in signal structure in suboscine birds exposed to anthropogenic noise. Vocal frequency characteristics of the noise-sensitive gray flycatcher appear uninfluenced by ambient noise amplitudes. In contrast, the noise-tolerant ash-throated flycatcher increases low frequency features of its vocalizations with increased background noise amplitude. The differences observed for these two species suggest that signal frequency change may be a mechanism that permits some species to inhabit noisy environments, yet those species unable to alter signal frequency may be functionally silenced and abandon noisy areas (Slabbekoorn & Peet 2003). We elaborate on these possibilities below.

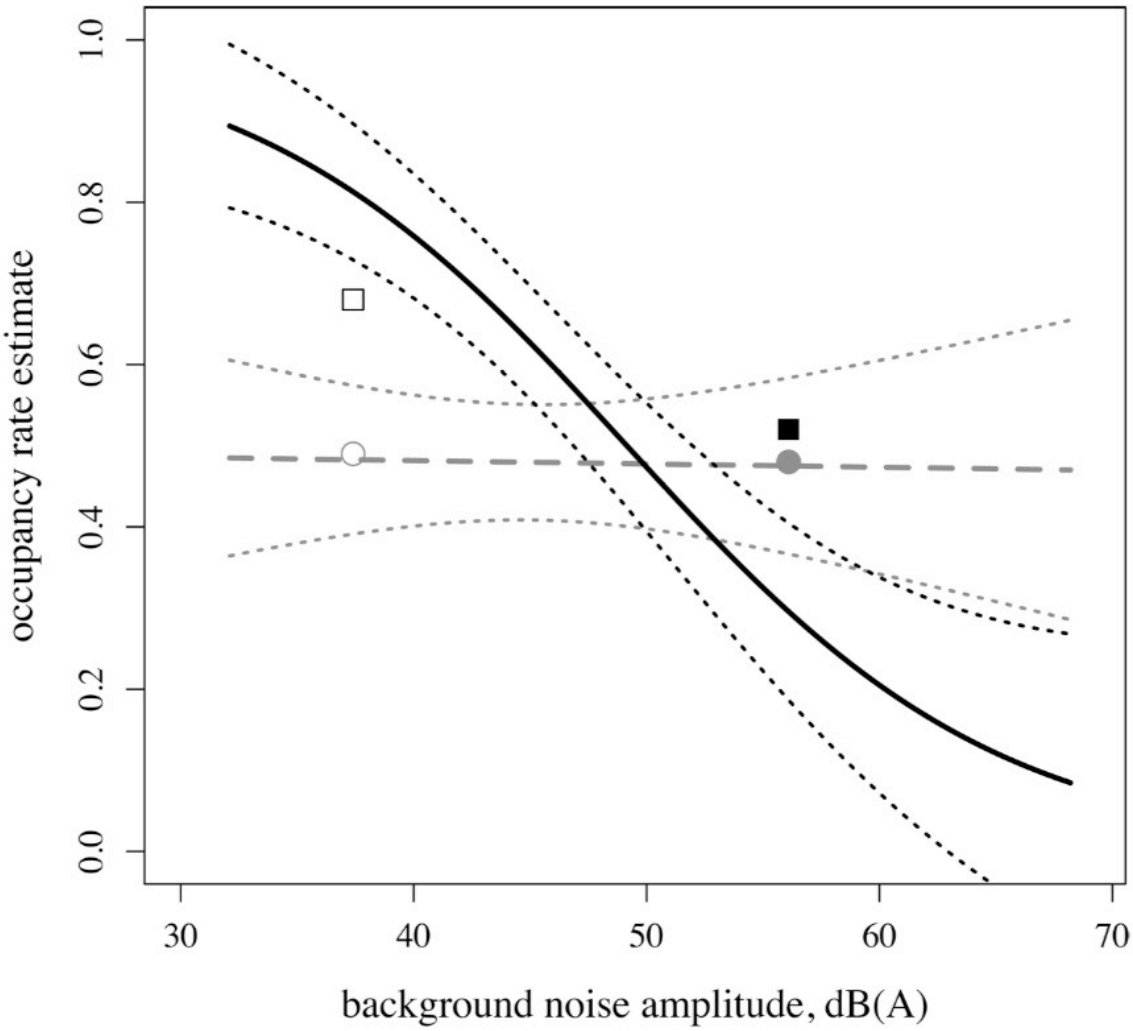


Figure 5.5 The occupancy rate estimate for gray flycatchers declined significantly with increased noise amplitude at the point count locations (solid black line). Ash-throated flycatcher occupancy was not significantly affected by noise amplitude (bold gray long dashed-line). Small dashed lines denote 95% confidence intervals for occupancy estimates with respect to noise amplitude. Points are located at the mean noise amplitude on each site-type and represent the proportion of point count locations where gray flycatchers (black circles) and ash-throated flycatchers (gray squares) were detected on treatment sites (filled symbols) and control sites (open symbols).

Table 5.1 Results from regression analyses using background noise amplitude to predict spectral characteristics for ash-throated flycatcher song (n = 26) and call (n = 21). Significant values, after Bonferroni correction was applied for multiple comparisons, are indicated with asterisks. See Table 5.2 for complete results for the gray flycatcher.

	song		call	
spectral feature	**R^2**	***p***	**R^2**	***p***
minimum frequency	0.123	0.045	0.382	0.002*
maximum frequency	0.024	0.216	0.042	0.670
peak frequency	0.091	0.073	0.052	0.932
lowest-note peak frequency	0.304	0.002*	0.296	0.006*
bandwidth	0.033	0.657	0.261	0.010*

Table 5.2 Results of regression analysis using background noise amplitude (dB(A)) to predict spectral characteristics for gray flycatcher song (n = 22) and call (n = 22). Significant values, after Bonferroni correction was applied for multiple comparisons, are indicated with asterisks.

	song		call	
spectral feature	**R^2**	***p***	**R^2**	***p***
minimum frequency	0.050	0.963	0.048	0.834
maximum frequency	0.079	0.110	0.043	0.719
peak frequency	0.050	0.945	0.021	0.243
lowest-note peak frequency	0.050	0.953	0.049	0.909
bandwidth	0.028	0.521	0.050	0.934

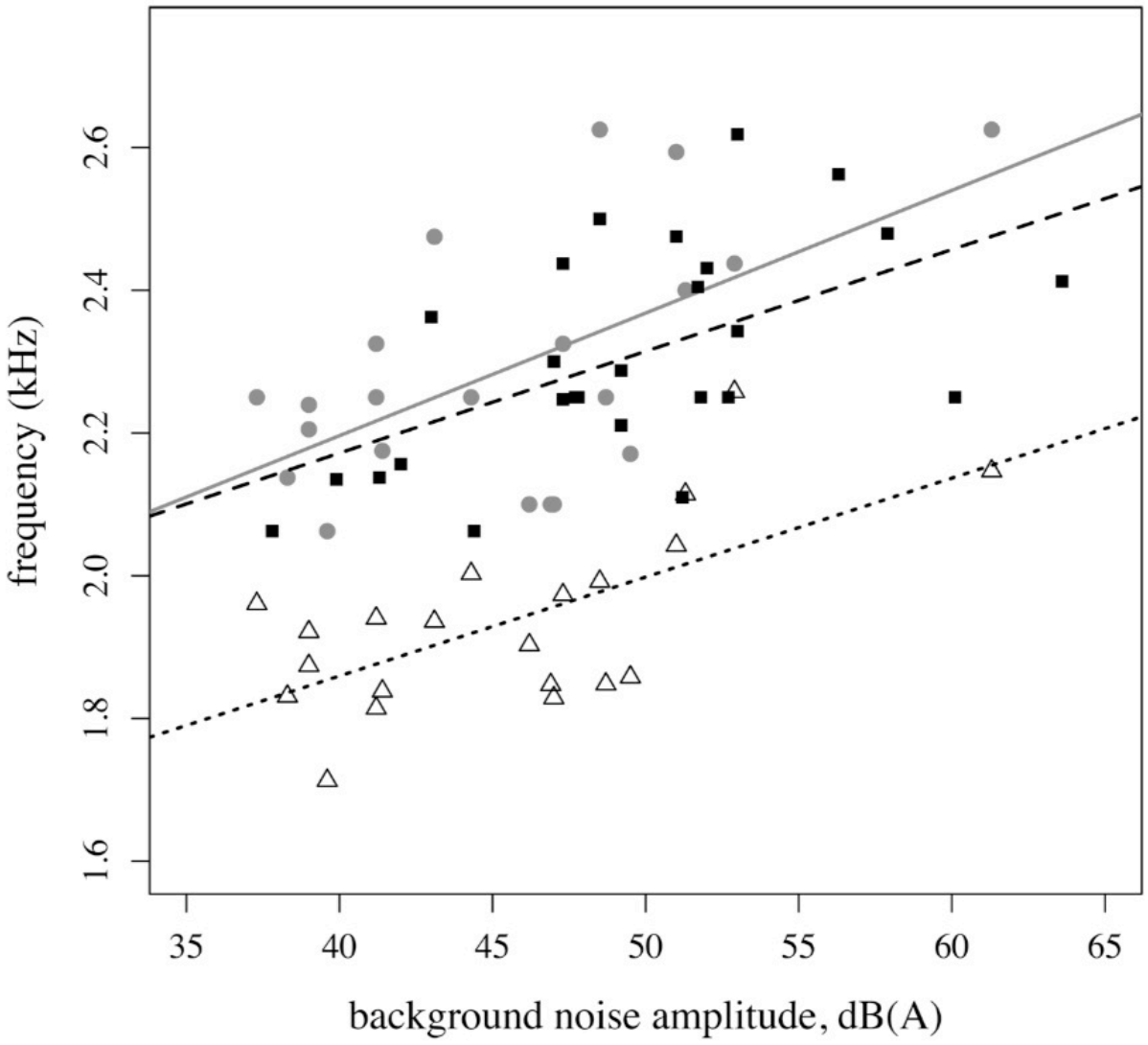


Figure 5.6 Relationship between ash-throated flycatcher vocal frequency (kHz) and background noise amplitude (dB(A)) measured at the location of the individual. Peak frequency of the lowest note for songs (black squares and long-dashed line) and calls (gray circles and solid gray line), plus call minimum frequency (open triangles and short-dashed line), all increased with background noise amplitudes.

The two species examined here vocalize at different frequencies; therefore, noise may not represent an equivalent source of acoustic interference for each. The ash-throated flycatcher's lower frequency vocalizations should suffer from a greater degree of acoustic masking by low frequency noise than the gray flycatcher, and thus it might be expected to have a stronger negative response to noise in terms of habitat use or it may alter vocal attributes in response to acoustic masking. For example, a recent study examining the influence of traffic noise on Australian songbirds found the low-frequency singing grey shrike-thrush (*Colluricincla harmonica*) to sing at a higher frequency in the presence of traffic noise, yet the higher pitched singing grey fantail (*Rhipidura fuliginosa*) did not shift song frequency in noise (Parris & Schneider 2009). Detections of both species declined with increased traffic noise, but the authors were unable to determine whether this pattern was the result of declines in abundance as a result of traffic noise or a reduced probability of detection by the observer with increased traffic noise. Here we controlled for the influence of noise on detections by turning compressors off during surveys and found ash-throated flycatchers to sing at a higher pitch with increased background noise, but not to avoid noisy areas. In contrast, gray flycatchers tended to avoid noisy regions, as expected from the pattern of noise avoidance in their nest placement (Francis et al. 2009). Yet even those gray flycatchers recorded vocalizing in noisy areas (as high as 62.6 dB(A)) do not have different vocal spectral features than those vocalizing in quiet areas. Though the gray flycatcher's higher pitched vocalizations may suffer less acoustic masking from low frequency compressor noise, their vocalizations may still be functionally masked when vocalizing

at low amplitudes or when near gas wells compressors where background noise has considerable energy above 5 kHz (Figures 5.2 & 5.3).

The frequency shifts observed for low-pitched features of ash-throated flycatcher vocalizations may be expected because low frequencies suffer most from acoustic masking from low-pitched anthropogenic noise. Several recent studies have also found frequency shifts among low-frequency song features in oscine birds and the magnitude of the frequency change observed in this study (≈ 200 Hz) is similar to other reported shifts. For example, the minimum frequency of urban great tit songs was approximately 200 Hz higher than that of great tit songs in forested habitats (Slabbekoorn & den Boer-Visser 2006) and two separate studies report that urban European blackbird's (*Turdus merula*) sing the low-pitched motif section of their song at roughly 120-200 Hz higher than blackbirds from forested areas (Nemeth & Brumm 2009; Ripmeester et al. 2010). A shift of 200 Hz has also been observed for chiffchaffs (*Phylloscopus collybita*) near highways relative to those near rivers (Verzijden et al. 2010) and reed buntings appear to shift the minimum frequency of their songs up 500 Hz in noisy areas (Gross et al. 2010). Whether other species may be capable of larger noise-dependent frequency shifts is unknown, but the repeated documentation of relatively small frequency shifts may reflect common constraints to frequency change in passerine birds in response to masking by anthropogenic noise or may even represent a physiological side effect of changes in vocal amplitude (see below; Nemeth & Brumm 2010). Additionally, these small frequency shifts may only slightly improve communication in noisy environments (Nemeth & Brumm 2010). More research documenting whether other oscine and

suboscine birds are capable of noise-dependent signal shifts, plus the magnitude of such shifts, will greatly improve our understanding of what range of shifts may be expected in songbirds and whether such shifts effectively mitigate masking effects of noise.

Despite the growing body of literature that has compared songs of urban and rural birds to show that birds modify the pitch of their song in response to noise, differences in song pitch may instead be the result of a change in the physical structure of the environment or motivational state of the signaler (Nemeth & Brumm 2009). Cities have less frequency absorbing and reverberating features, such as those in forests where lower frequencies are optimal for sound transmission. Additionally, motivational state could be higher when social interactions are more intense, such as in high-density urban bird populations. Here, we show that ash-throated flycatcher vocalizations are higher with increased background noise independent of changes to the physical structure of the habitat because vegetation features, such as tree density or canopy cover, do not differ on treatment an control sites (Francis et al. 2009). We also found no evidence for changes in ash-throated flycatcher occupancy with respect to noise amplitude, suggesting no change in density that may influence motivational state and vocal frequency.

There are several other potential mechanisms that may explain the higher minimum frequencies observed for ash-throated flycatchers vocalizing in increased background noise and include evolutionary, ontogenetic or behavioral modifications (Patricelli & Blickley 2006; Halfwerk & Slabbekoorn 2009). Because song is innate in

tyrant flycatchers (Kroodsma 1984, 2004), ontogenetic changes during song acquisition (i.e., learning) are unlikely. A long-term adaptive explanation via natural selection is also possible, but this mechanism may also be unlikely due to the scattered spatial arrangement of compressors throughout our study area. Unlike urban areas, where vast regions may have elevated background noise amplitudes relative to the surrounding landscape, our study area is characterized by point sources of elevated background noise in a relatively quiet landscape; thus this patchy distribution of noisy habitat is unlikely to support a divergent population. Another possible explanation for the observed patterns could be intraspecific differences in vocal frequencies at the level of the population, where individuals with particular vocal frequencies settle in habitats where their signals may be successfully dispatched. For example, larger-bodied birds with lower-pitched vocalizations may tend to settle in relatively quiet habitats and smaller individuals that vocalize at a higher pitch occupy noisier areas. Unfortunately, data on individual body sizes is not available and we could not evaluate this possibility.

Short-term behavioral modifications may be a more likely explanation for the observed frequency changes, and noise-dependent modifications at the level of the individual have been documented in several oscine birds, including great tits (Halfwerk & Slabbekoorn 2009), chiffchaffs (Verzijden et al. 2010), and reed buntings (Gross et al. 2010). Though tyrant flycatcher song may develop normally in the absence of learning, this does not necessarily mean that individuals may be incapable of small adjustments to innate signals in response to environmental conditions and other stimuli. For example, ocellated antbirds (*Phaenostictus mcleannani*) increase the pitch of their

vocalizations during aggressive encounters (Araya-Ajoy et al. 2009). In the case of noise-dependent signal adjustments, signal modifications would require a signaler to detect masking of a signal and alter the vocalization in such a way that it increases detection by receivers (Patricelli & Blickley 2006). However, critical tests to determine whether ash-throated flycatcher and other suboscine individuals adjust vocal frequency in response to acoustic masking are needed.

Another plausible mechanistic explanation for the frequency shift in background noise is that frequency shifts are by-products of shifts to a different vocal attribute: amplitude. Increases in frequency coupled with increased vocal amplitude have been observed in humans (Junqua 1993; Traunmüller & Eriksson 2000), frogs (Lopez et al. 1988) and non-passerine birds (Beckers et al. 2003). Additionally, increases in vocal amplitude with increased noise (Lombard effect) appear common in mammals and many birds (*reviewed in* Brumm & Slabbekoorn 2005). It is possible that the small frequency shifts observed in this and other studies may be consequences of increases in vocal amplitude, rather than short- or long-term adaptations to overcome the masking effects of noise (Nemeth & Brumm 2010). Unfortunately, however, accurate measurement of vocal amplitude in the field is challenging and requires measurement from directly below the individual to control for the directional radiation of vocal sound waves (Brumm 2004). Studies using captive birds that can simultaneously measure amplitude, spectral and temporal changes to vocalizations in response to noise may prove to be especially fruitful in identifying which vocal features may co-vary with signal adjustments.

Our data show a clear difference in species' responses to noise in terms of habitat use, plus differences in patterns of vocal frequency with respect to background noise amplitude and masking potential. These results suggest that generalizations across species regarding sensitivities to noise and vocal changes in response to acoustic masking may be limited. Growing evidence from single-species studies suggest that noise-dependent signal change may be quite common in oscine birds (e.g., Slabbekoorn & Peet 2003; Verzijden et al. 2010; Gross et al. 2010). In this study we see very different responses to noise from representatives of two different subfamilies within Tyrannidae (families Tyranninae and Fluvicolinae), suggesting that not all tyrant flycatchers respond to anthropogenic noise in the same manner, both in terms of habitat use and vocal frequency patterns. Whether more closely related species tend to have similar responses is still unknown.

A fundamental next step is to begin to evaluate the phylogenetic distribution of responses to anthropogenic noise through multi-species studies, both in terms of habitat selection and vocal change. We expect that closely related species will have a shared suite of similar vocal traits and that members of individual lineages might show comparable responses to noise. Understanding if and to what degree responses are phylogenetically conserved will greatly improve our ability to determine which lineages and species can cope with acoustic interference from anthropogenic noise and which are muted by industrial clamor and disappear from the increasing number of habitats afflicted by human noise.

CHAPTER VI

LANDSCAPE PATTERNS OF AVIAN HABITAT USE, AND NEST SUCCESS RESULTING FROM CHRONIC GAS WELL COMPRESSOR NOISE IN NW NEW MEXICO, USA.

ABSTRACT

Anthropogenic noise is becoming a dominant component of soundscapes across the world and these altered acoustic conditions may have severe consequences for natural communities. We modeled noise amplitudes from gas well compressors across a 16 km^2 study area to estimate the influence of noise on avian habitat use and nest success. Using species with noise responses representative of other avian community members, across the study area we estimated gray flycatcher (*Empidonax wrightii)* and western scrub-jay (*Aphelocoma californica*) habitat occupancy, and flycatcher nest success, which is highly dependent on predation by jays. We also explore how alternative noise management and mitigation scenarios may reduce area impacted by noise. Compressor noise affected 84.5% of our study area and occupancy of each species was approximately 5% lower than would be expected without compressor noise. In contrast, flycatcher nest success was 7% higher, reflecting a decreased rate of predation in noisy habitat. Not all alternative management and mitigation scenarios reduced the proportion of area affected by noise; however, use of sound barrier walls around compressors could reduce the area affected by noise by 70% and maintain

habitat occupancy and nest success rates at levels close to those expected in a landscape without compressor noise. These results suggest that noise from compressors could be effectively managed and, because habitat use and nest success are only two of many ecological processes that may change with noise exposure, minimizing the anthropogenic component of soundscapes should be a conservation priority.

INTRODUCTION

Human activities have transformed earth's land surfaces, greatly altering species distributions and ecological processes across vast landscapes (Vitousek et al. 1997; Grimm et al. 2008). Traditionally, ecologists have focused on changes most obvious to the eye: changes in vegetation, alterations of population dynamics, reductions of biodiversity, and changes to other more-readily observable ecological processes (Fahrig 2003; Ewers & Didham 2006). Many studies have not focus on the more obscure, but potentially important, components of human disturbance, such as anthropogenic noise (hereafter, "noise"). Yet a recent surge of studies investigating the influence of noise on wildlife has shown that noise may have severe negative consequences for a diverse array of taxa (*reviewed in* Barber et al. 2010). Though evidence for impacts of noise on natural communities is growing, and the scale to which noise penetrates natural habitats is extensive (Barber et al. 2010), to date, studies have not examined ecological changes in response to noise at broad-scales.

There have been two main research directions involving consequences of noise on wildlife, but neither has focused on broad-scale patterns (i.e., > 100s ha). First, a number of studies have focused on how noise disrupts acoustic communication by masking acoustic signals and, in turn, how animals adjust signals to mitigate the masking effects of noise (e.g., Slabbekoorn & Peet 2003; Gross et al. 2010). These studies have primarily focused on birds, but amphibians and terrestrial mammals have also received attention (e.g., Rabin et al. 2006; Egnor et al. 2009; Parris et al. 2009). A second direction has involved the influence of noise on species abundances and densities. A long line of studies suggests that noise from roadways may exclude species from otherwise suitable habitat (e.g., Reijnen et al. 1995; Forman et al. 2002; Rheindt 2003), but most findings have been confounded by uncontrolled variables associated with human-generated noise. For example, noise caused by traffic co-varies with changes in vegetation, edge effects, moving vehicles, pollution intensity, and mortalities from animal-vehicle collisions. In urban habitats, many of these same features may change as acoustics vary across the landscape, but species common to urban areas have broader environmental tolerances than species that avoid urban areas (Bonier et al. 2007); therefore, responses by these species may not represent typical responses within a taxon. More recent studies that controlled for confounding factors associated with urban and roadway habitats, and without focusing on species common to urban areas, have shown that noise may not only reduce bird habitat use (Bayne et al. 2008) and pairing success (Habib et al. 2007), but may also change avian communities and predator-prey interactions (Francis et al. 2009).

All landscapes include soundscapes, which are the dynamic acoustic environments that characterize different locations (Schafer 1977). These sounds may include biological sounds, sounds from moving abiotic features (e.g., wind, rain, water), as well as anthropogenic sounds. A critical step to understanding the full impacts of the anthropogenic component of soundscapes is to characterize the magnitude of noise disturbances on a landscape level and determine how these altered acoustics impact natural communities. Understanding these ecological processes at a landscape level will also contribute to our understanding of potential effects on population regulators (e.g., predators, diseases, and parasites), ecological services (e.g., pollination and seed dispersal), keystone species, and movements (e.g., gene flow, dispersal paths, and migration corridors). With this understanding, we may then be able to determine best management practices that can realistically be implemented to mitigate the negative effects of noise across landscapes.

Here, we aim to (i) quantify the anthropogenic component of a soundscape resulting from gas well compressor noise, (ii) pair landscape-level acoustic patterns with avian habitat use and nest success, and (iii) evaluate how acoustic and ecological patterns change under alternative energy extraction management practices and mitigation scenarios. First, we evaluate several candidate models that predict compressor noise amplitude with respect to distance from source and use the best model to map noise amplitudes across a 16 km^2 study area representative of our study region. Our goal is to provide amplitude values that are representative of the region as a whole. Second, to illustrate how compressor noise can alter ecological processes

across a large area, we use predictions from our noise amplitude model to calculate broad-scale habitat occupancy rates for two species, the gray flycatcher (*Empidonax wrightii*) and western scrub-jay (*Aphelocoma californica*). We also evaluate nest success for gray flycatchers, which is highly dependent on predation by western scrub-jays (Francis et al. 2009). Finally, we examine how several alternative mitigation and management practices may restore a more natural soundscape by decreasing the proportion of the landscape impacted by compressor noise.

METHODS

Study Area & Noise Measurements

The study area covered approximately 16 km^2 in Rattlesnake Canyon Habitat Management Area (RCHMA), located in northwestern New Mexico, United States of America. The area is dominated by piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands and, to a lesser degree, open sagebrush (*Artemesia tridentata*) grasslands. RCHMA is managed by the Bureau of Land Management (BLM) and is within the southern half of the San Juan Basin, one of the nation's most developed energy producing regions (BLM 2003). In contrast to many regions producing natural gas, gas wells in RCHMA are often coupled with compressors (referred to as "wellhead compression"). This pairing of compressors on individual wells creates numerous point sources of compressor noise across the landscape (Figure 6.1). Instead of wellhead compression, other gas producing regions may have central compression, in which numerous compressors are clumped in one location and service many wells

within an area. Both types serve the same purpose: aiding in the extraction and transportation of gas through pipelines. In either arrangement, compressors run 24 hours a day, 365 days a year aside from periodic maintenance and during our bird surveys and nest searches (see below, Francis et al. 2009).

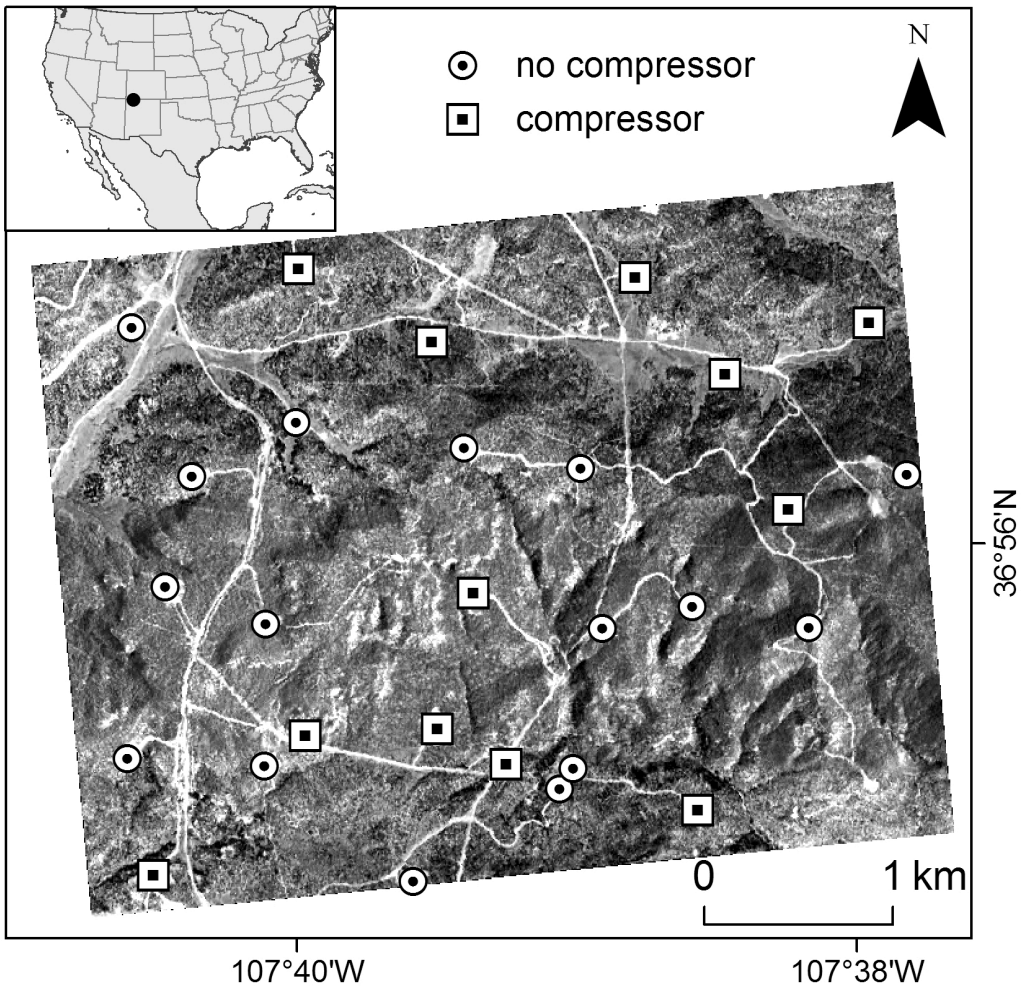


Figure 6.1 Location of the 16 km^2 study area in Rattlesnake Canyon Habitat Management Area (RCHMA), San Juan County, New Mexico, and spatial distribution of wells with and without compressors.

For previous studies, we had used the arrangement of well pads with noise-generating compressors (treatment sites) and well pads without compressors (control sites) to determine the influence of compressor noise on natural avian populations and communities. Unlike studies along roadways (Reijnen et al. 1995; Forman et al. 2002; Rheindt 2003) or in urban areas (Nemeth & Brumm 2009), human activity and vegetation does not differ on and around well pads with and without compressors (Francis et al. 2009). Therefore, effects of noise are separated from other confounding variables that complicate numerous studies that have investigated the influence of noise on wildlife along roadways or along urban gradients. Additionally, compressors were turned off for two hours during surveys and nest searches so that noise would not bias our ability to locate nests or birds.

We chose our study area extent because it is representative of well (≈ 1.78 ± 0.34 SD per km^2) and compressor densities (0.81 ± 0.25 SD per km^2) throughout RCHMA (Francis, unpublished data) and may serve as initial values to estimate the full extent of noise exposure in the gas-producing region. Our study area included 28 active wells (1.74 per km^2) and 12 active compressors (0.75 per km^2) in 2005 (Figure 6.1). Habitat surrounding three of these wells was used for our nesting study (Francis et al. 2009), and roughly half were used for related studies (Francis, unpublished data). In habitat surrounding these study sites, plus that of over 70 wells outside the area under consideration here, we measured compressor noise amplitudes and at a subset of these sites, we also recorded background noise using a Marantz PMD 660 Digital recorder using a directional shotgun microphone (Audio-technica AT-815). For all measurements,

the distance from the nearest compressor (on treatment sites) or wellhead (on control sites) was recorded. Noise amplitude measurements were taken with NIST certified sound pressure meters (Casella® model CEL 320 and CEL 1002 converter) for approximately two minutes and, for most locations, on three separate occasions (different days and times) to control for the effects of atmospheric variability on amplitudes. Measurements were discarded and retaken when aircraft noise was audible, when birds were vocalizing within ≈ 30 m, which could bias measurements, and when wind conditions reached category three (≈ 13-18 km/h) on the Beaufort Wind Scale.

Noise amplitude models

To estimate noise amplitudes across the study area, we used mean noise amplitude measurements from 1140 individual locations in piñon-juniper habitat ranging from 2 to 517 m from gas wells (on control sites) and compressors (on treatment sites) near 86 different wells. The typical ambient noise amplitude uninfluenced by compressor noise was assigned as 55.00 ± 0.14 SE dB(C), calculated as the mean value from measurements at 541 locations surrounding quiet control sites. Hereafter we refer to this value as baseline amplitude. To characterize those areas where noise amplitudes have been increased due to compressor noise, we evaluated the strength of support for several candidate models predicting noise as a function of distance from the source. Our candidate models considered noise amplitude as (i) a linear function of distance (linear), (ii) a power function of distance (power), (iii) a natural logarithm of distance

($\log_e$), (iv) an exponential decay function of distance ($e^{distance}$), and (v) a null intercept only model in which noise was unrelated to distance from the source (null). For all models considered (except null), we estimated not only the distance coefficient, but also the amplitude at the source because we lacked noise measurements at a distance of zero meters.

For our model selection procedure, we used an information-theoretic approach to evaluate support for competing candidate models (Burnham & Anderson 2002) with Akaike's Information Criterion corrected for small sample sizes (AIC_c). We ranked models based on differences in AIC_c scores (ΔAIC_c). Candidate models with ΔAIC_c scores within two of the best models were considered to have strong support, and those within four ΔAIC_c were considered to have some support. All analyses were performed in R (R Development Core Team, 2009).

Noise, Occupancy and Nest Survival Spatial Analyses

Utilizing the best-supported noise model we computed the area affected by compressor noise within the study area. Compressors that could have sound waves that extend into the study area but were not located within its boundaries were excluded from the analysis. Noise amplitudes were mapped as multiple circular concentric buffers from the compressor location using 2 dB(C) intervals and the area affected by each amplitude bin was calculated. Subsequently, we computed the cumulative proportion of area affected by each of these amplitude intervals. However, for visual clarity we used 5 dB(C) intervals for generating the maps. Because baseline ambient noise amplitude in

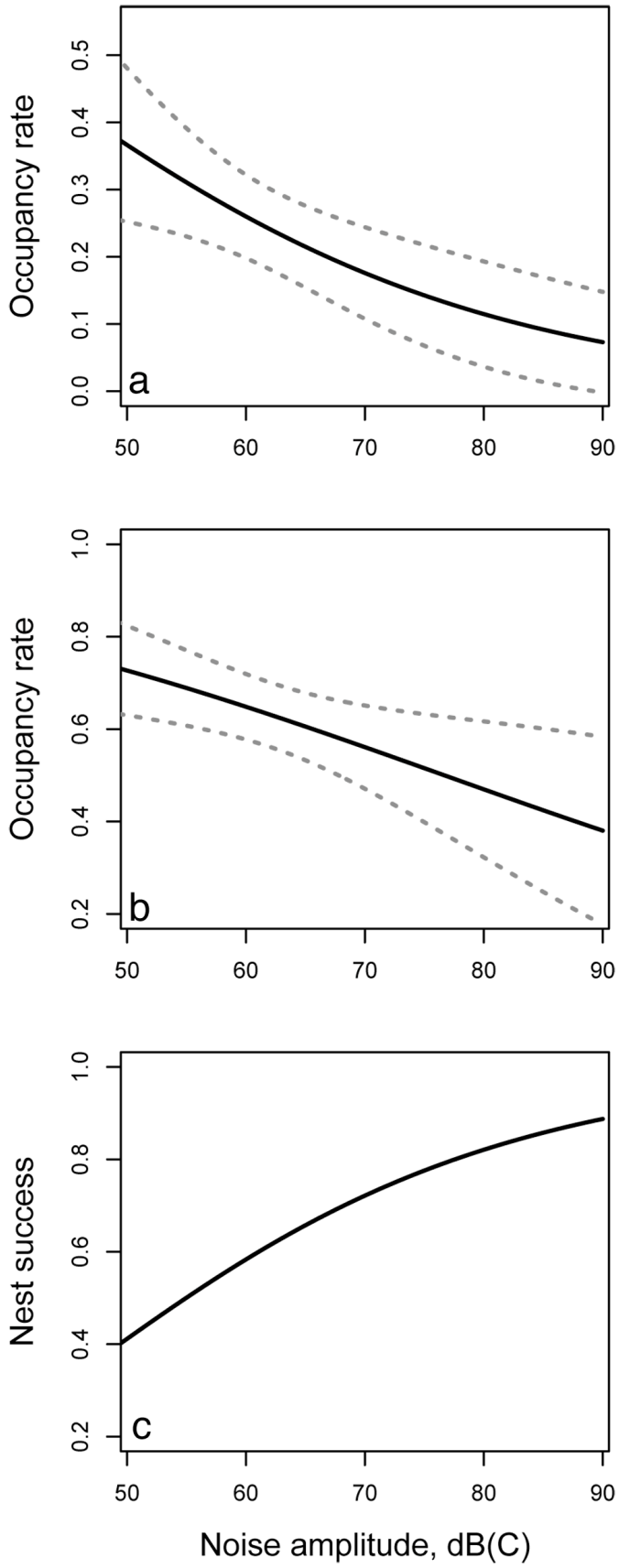
the study area is 55 dB(C), we used this value as the sound matrix in which noise from the compressors were embedded.

The empirically derived model for noise used here implicitly accounts for topography and vegetation, thus we did not include these variables when computing area affected by noise across space. The relatively small area in which noise from two or more compressors overlap and the low increase in amplitude in these overlapping areas did not always necessitate inclusion of modifications in the model to account for noise overlaps; therefore, we made no attempt to combine noise amplitudes from multiple sources and the values we report here are conservatively low. All spatial analyses were conducted using ArcGis 9.3 (ESRI 2008).

Habitat occupancy estimates for gray flycatchers and western scrub-jays were based on our previous findings suggesting that compressor noise negatively influences occupancy (Francis et al. 2009; Chapter V; Figure 6.2a-b). Nest survival estimates are based on daily nest survival (DNS) estimates using the logistic-exposure method (Shaffer 2004). However, because we were most interested in examining spatial patterns of predation risk, we excluded all nests that failed for other reasons and have modeled nest success using only those nests that successfully fledged one or more young or failed to predation; therefore, here, measures of nest success reflect a nest's probability of not failing to predation (Francis et al. 2009). This was justified because flycatcher nest abandonment was very low in our study and did not differ between sites (4% on noisy sites and 3% on quiet sites). For ease of interpretation, we display these estimates as predicted nest success for the entire 30-day nesting cycle that is typical of

gray flycatchers (Sterling 1999; Figure 6.2c). We linked the variation in occupancy and nesting success based on changes in noise amplitude to our noise maps and calculated weighted mean habitat occupancy rates and nest success estimates across the study area. Because areas affected by noise amplitudes were estimated in 2 dB(C) intervals, we used occupancy rates and nest success estimates based on the lowest dB(C) value for each interval.

Figure 6.2 Patterns of habitat occupancy and nest success that vary with noise amplitude. Western scrub-jay occupancy declines with increased noise amplitude (generalized linear mixed model with binomial errors [GLMER], occupancy β_{dB} = -0.05 ± 0.02 SE, P = 0.006) (**a**), as does gray flycatcher occupancy (GLMER, occupancy β_{dB} = -0.06 ± 0.02 SE, P = 0.018) (**b**). In contrast, gray flycatcher nest success (nests surviving that did not fail to predation) increases with noise amplitude (generalized linear model [glm], binomial errors, logistic-exposure link, DNS β_{dB} = 0.06 ± 0.04 SE, P = 0.004) (**c**).


Occupancy rate
0.0
0.1
0.2
0.3
0.4
0.5
a
50
60
70
80
90
Occupancy rate
0.2
0.4
0.6
0.8
1.0
b
50
60
70
80
90
Nest success
0.2
0.4
0.6
0.8
1.0
c
50
60
70
80
90
Noise amplitude, dB(C)

Alternative management and mitigation scenarios

The alternative noise management and mitigation scenarios we considered involved (i) sound barrier walls around compressors located on existing wells, (ii) a central compression station resulting in a single point source of compressor noise (multiple tightly-grouped compressors) rather than many across the landscape (Figure 6.1), and (iii) a central compression station surrounded by sound barrier walls.

Noise mitigation with sound barrier walls exists in a few areas of RCHMA where wells are adjacent to residential property (C. D. Francis, pers. obs.). Though compressors with sound barrier walls are often encased on all four sides, in some cases barriers encase compressors on only three sides. We measured amplitude at 30 m behind walls on three sides and on one side lacking the barrier and found that amplitudes on open sides (81.11 ± 0.61 SE dB(C), $n = 4$ wells) were similar to those measured on compressors lacking barriers (81.94 ± 0.55 SE dB(C), $n = 9$ wells; two-tailed $t = 0.92$, df = 11, $p = 0.38$) and that amplitudes on sides with walls were roughly 10 dB(C) lower than open sides (71.23 ± 0.56 SE dB(C), $n = 4$ wells; two-tailed $t = 17.76$, df = 6, $p < 0.001$). Based on these measurements, we mapped noise amplitudes assuming that noise barrier walls reduce noise by 10 dB(C) at a distance of 30 m from the compressor on all sides (assuming four-sided noise barriers). Here we used the top-model describing noise amplitudes but adjusted the noise at the source to achieve a 10 dB(C) reduction at 30 m.

Central compression may service dozens to hundreds of individual wells; for example, in the northern San Juan Basin a single central compressor station services

30 individual wells (V. Rudolph, Peak Energy Resources, pers. comm.). To model this scenario, we assumed (i) that because 12 compressors were located across the sample landscape, 12 compressors would be required on the compressor station and (ii) though amplitude at the source of each compressor may differ slightly, we assumed that amplitudes at all 12 compressors are equal so that we may calculate the increase in amplitude over that of a single source as:

$$\Delta \text{dB} = 10 \times \log_{10} n \quad (1)$$

where ΔdB is the increase in amplitude, and *n* denotes the number of sources. Thus, amplitude will be 10.79 dB(C) greater at the source at compressor stations over the wellhead compression observed at our sites. We used the same top-model to map noise amplitudes across the landscape, but adjust amplitude at the source at 10.79 dB(C) greater than on individual wells.

Finally, use of noise barrier walls on compressor stations is also realistic. In a third scenario, we assume noise levels can also be reduced by 10 dB(C) at 30 m from the central compressor station and map the results with the top-model.

RESULTS

Noise amplitude models

The model describing noise amplitude as a function of the natural log of distance was best supported by the data, and no other models received support (Table 6.1). This model estimated amplitude at the compressor to be 106.83 dB(C) ± 0.93 SE and the attenuation coefficient to be -7.61 ± 0.19 SE. Using this model, compressor noise

amplitude does not attenuate to baseline amplitudes (55.0 dB(C)) found on control sites until 900 m from the compressor (Figure 6.3a). Additionally, most compressor noise above 5.0 kHz attenuates within the first few hundred meters of the source, and acoustic energy below 5.0 kHz dominates noise at larger distances from the source (Figure 6.3b-e).

Table 6.1 Results from model selection procedure describing noise amplitude (dB(C)) as a function of distance from the source using Akaike's information criteria adjusted for small sample size. *K* is the number of parameters in the model, AIC_c is Akaike's Information criteria for small sample size, ΔAIC_c is the difference in AIC_c values from the top-ranking model.

Candidate Models	***K***	**AIC_c**	**ΔAIC_c**
Log_e	3	3332.84	0.00
Power	3	3401.16	68.31
Exponential Decay	3	3549.73	216.89
Linear	3	3584.77	251.93
Null	2	4123.30	790.45

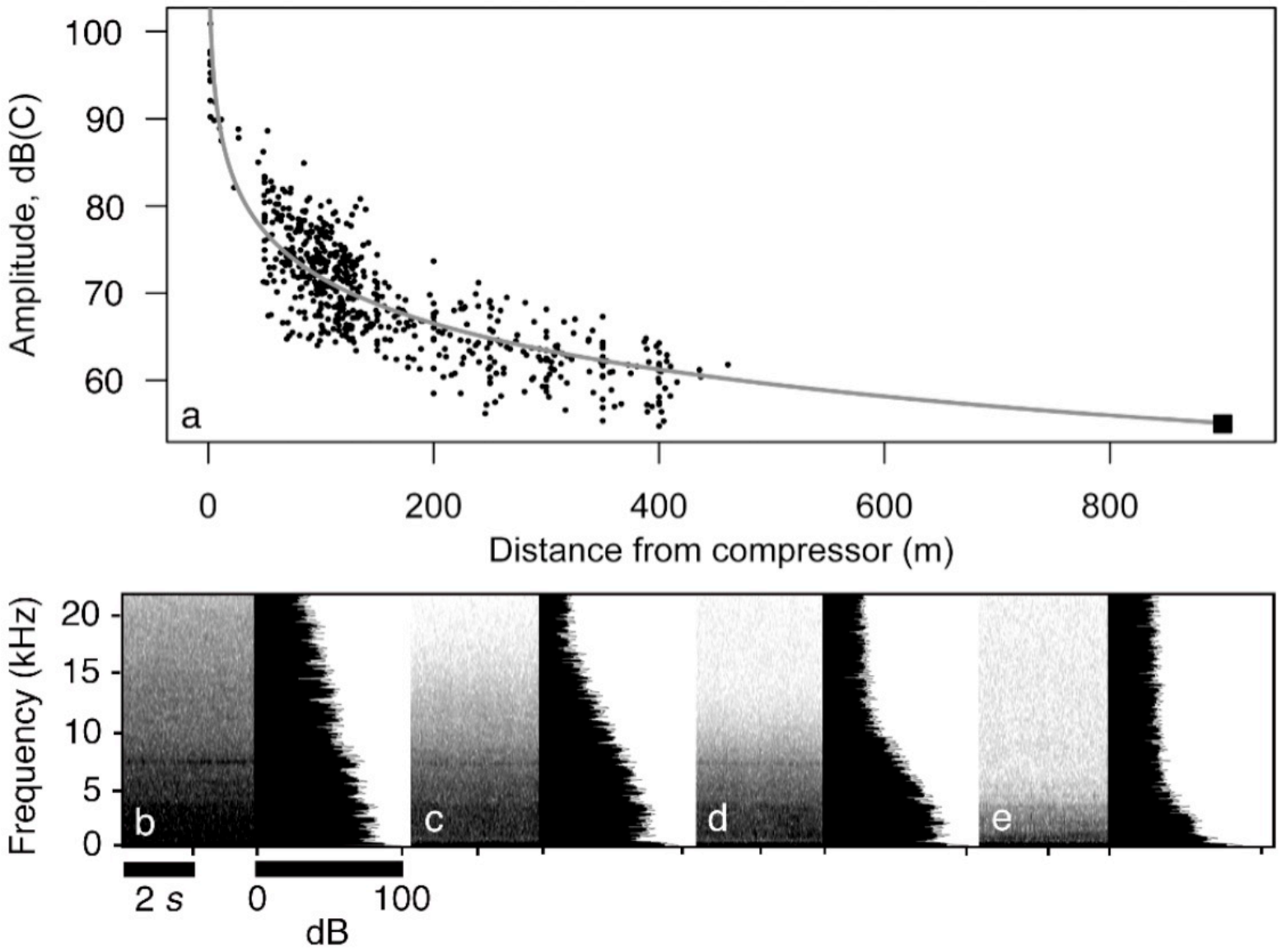

Amplitude, dB(C)
100
90
80
70
60
a
0
200
400
600
800
Distance from compressor (m)
Frequency (kHz)
20
15
10
5
0
b
c
d
e
2 s
0
100
dB

Figure 6.3 Noise amplitudes as described by the best model ($\log_e$ of distance from source) from 599 amplitude measurements (black circles) and spectrograms and power spectra displaying frequency content of compressor noise at various distances. (a) The top-model (solid gray line) predicts noise amplitude to attenuate to ambient values observed on control sites at a distance of 900 m from the compressor (large black square)(R^2 = 0.73). Compressor noise has considerable acoustic energy across a broadband of frequencies near the compressor. At 10 m (b), 50 m (c) and 100 m (d) there is considerable energy at higher frequencies, but the high frequency energy attenuates over shorter distances than low frequency noise. By 200 m (e) from the compressor, most of the acoustic energy is below ≈ 5 kHz.

Soundscape scenarios

Under the 2005 distribution of 12 wells with wellhead compression, the best noise model predicted that 1364 ha (84.5%) of the 1600 ha study area had amplitude levels higher than the baseline value (Figures. 6.4a & 6.5a). Approximately 14% of the area was exposed to amplitude levels a full order of magnitude higher in acoustic power (an increase of 10 dB) than the baseline level and 36% of the landscape experienced double the baseline sound pressure (an increase of 6 dB). In terms of listening area, which is the area surrounding an organism from which it may detect a signal, 61% of the landscape was exposed to noise amplitudes where the listening area was reduced by at least 50% (an increase of 3 dB; see Barber et al. 2010 for details).

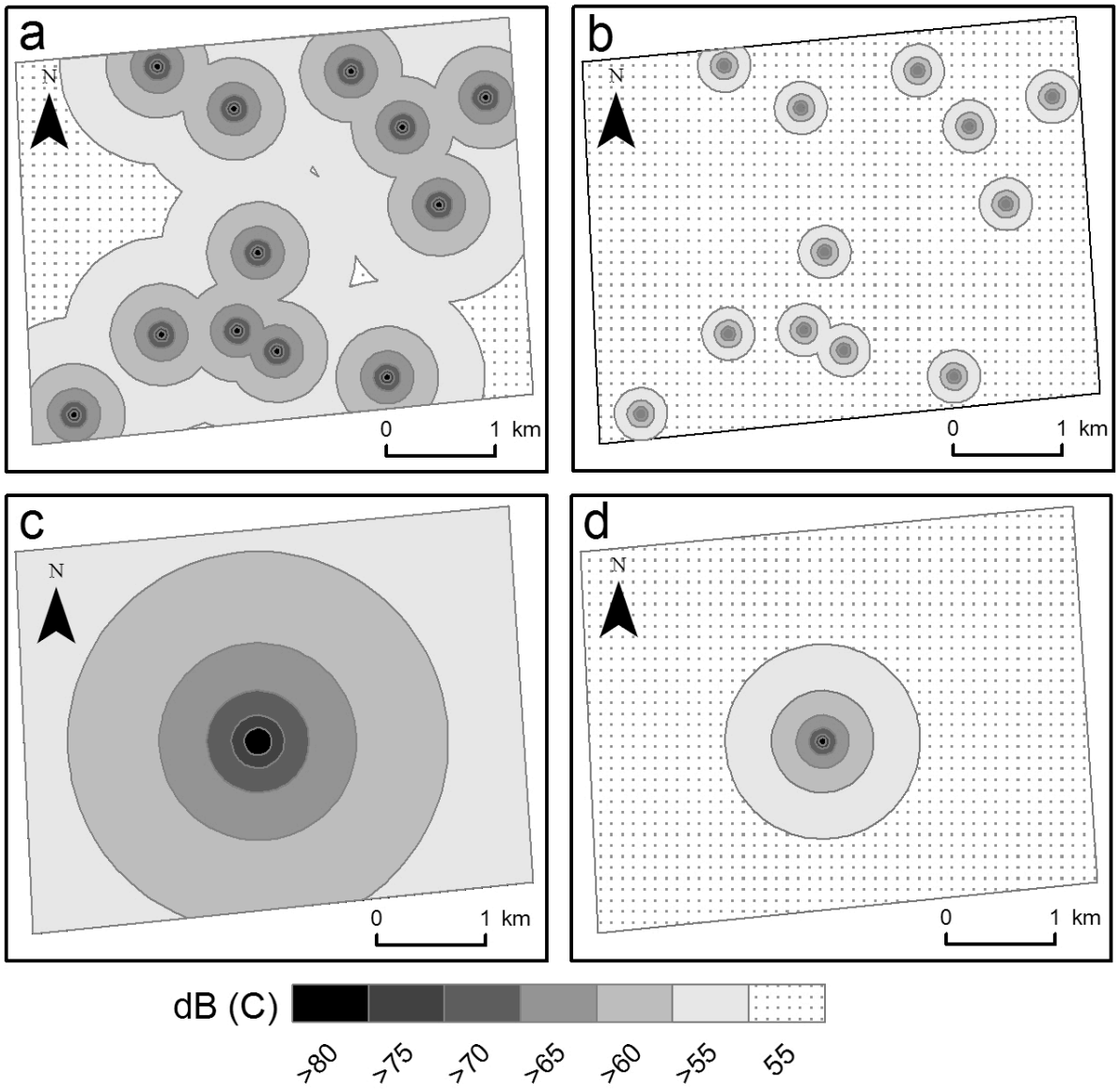
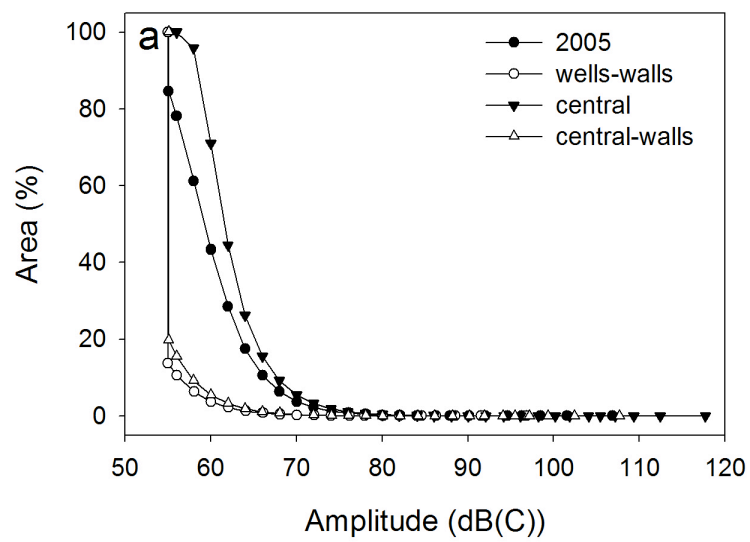
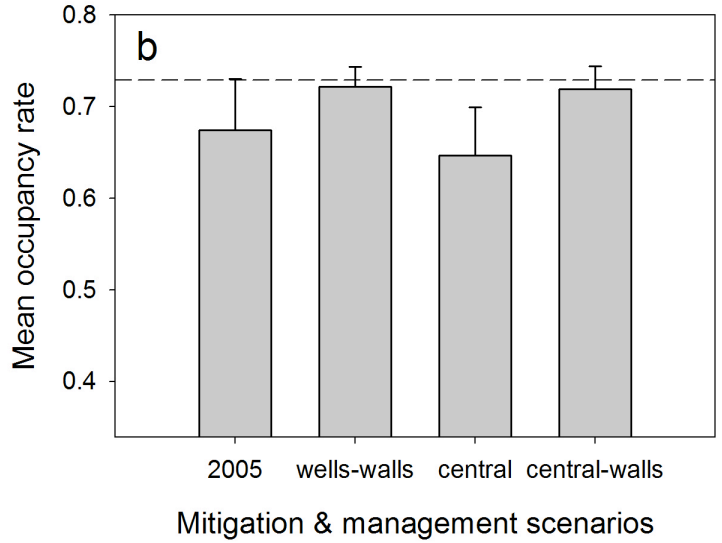
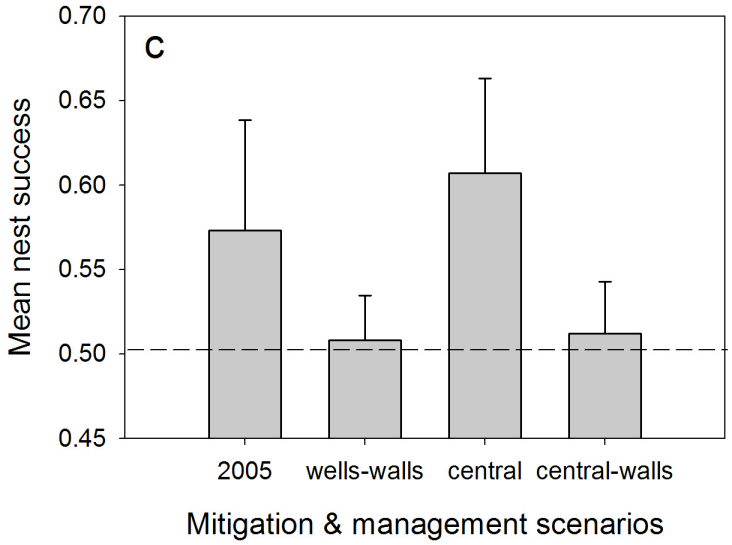


Figure 6.4 The extent and amplitude of noise exposure across the study area under conditions as documented in 2005 with wellhead compression (**a**), with noise reducing walls surrounding all compressors on individual wells (**b**), assuming central compression with 12 compressors clumped together (**c**), and as with (**c**) but with noise reducing walls surrounding the compressor station (**d**). Noise amplitudes have been placed in 5 dB(C) bins for visual clarity.


a
2005
wells-walls
central
central-walls
Area (%)
Amplitude (dB(C))


b
Mean occupancy rate
2005
wells-walls
central
central-walls
Mitigation & management scenarios


c
Mean nest success
2005
wells-walls
central
central-walls
Mitigation & management scenarios

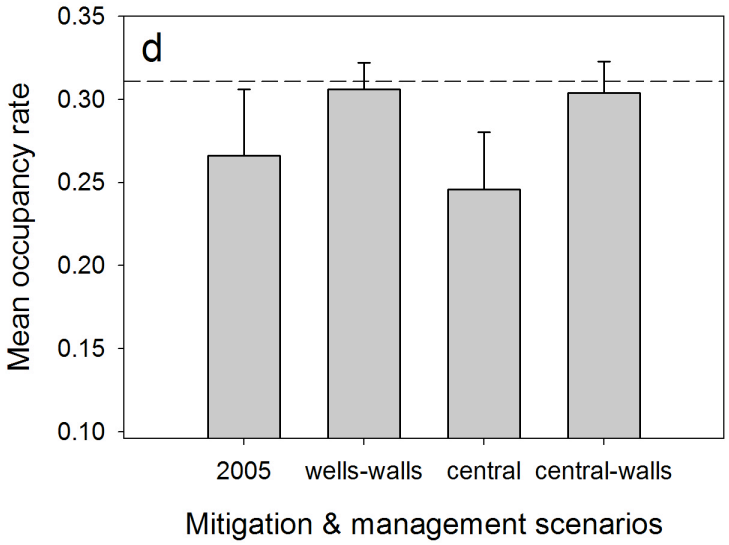

d
Mean occupancy rate
2005
wells-walls
central
central-walls
Mitigation & management scenarios

Figure 6.5 Comparisons of cumulative area exposed to noise at 2 dB(C) amplitude intervals and variation in occupancy and nest success under four management and mitigation scenarios. (**a**) The proportion of area exposed to noise amplitudes under each management scenarios. Western scrub-jay (**b**) and gray flycatcher (**d**) mean occupancy rates and gray flycatcher nest success (**c**) across the study area. Error bars denote SD. Horizontal dashed-lines indicate baseline values for occupancy and nest success in habitat uninfluenced by compressor noise. For (**a**-**c**) bars are labeled as follows: "2005" denotes wellhead compression observed in our study area, "wells-walls" is wellhead compression with noise-reducing walls, "central" is the central compression station scenario, and "central-walls" represents central compression and noise-reducing walls.

Of the three management scenarios, the alternatives with noise-reducing walls around individual wells with compressors and a central compression system resulted in the largest areas with baseline noise amplitudes (86.3% and 80.2% respectively; Figures 6.4 & 6.5a). These scenarios also had the smallest proportions of the landscape where the listening area was reduced by 50% or more (6.3% for individual compressors with walls and 9.2% for central compression with walls). The scenario with central compression without walls resulted in 100% of the spatial extent exposed to amplitudes above baseline values with over 58% of the area exposed to amplitudes at least double the sound pressure of the baseline level. Additionally, over 95% of the landscape had a reduced listening area of at least 50%.

Mean landscape-level occupancy and nest success estimates had subtle differences between conditions in 2005 and the three alternative scenarios. Mean occupancy rates for the western scrub-jay and gray flycatcher in the study area were predicted to be highest when noise-reducing walls surrounded individual wells with compressors (0.31 ± 0.02 SD and 0.72 ± 0.02 SD respectively); however, rates were

nearly as high for both species for central compression with noise-reducing walls (Figure 6.5). Moreover, rates were less than 0.05 higher than occupancy rates in 2005. Central compression without walls resulted in the lowest mean occupancy rates for both species. Gray flycatcher nest success was highest with central compression lacking walls, with approximately 0.61 ± 0.06 SD not failing to predation (Figure 6.5). Conditions in 2005 had the second highest prediction for the proportion of successful nests (0.57 ± 0.07 SD), and the two scenarios with noise-reducing walls had similar predictions for the proportion of successful nests across the extent (≈ 0.50 ± 0.03 SD each). It is also worth noting that the proportion of nests surviving for the two scenarios with noise-reducing walls would be roughly equivalent to the proportion of nests surviving at the baseline amplitudes observed on the quiet control sites (Figure 6.5c).

Discussion

Anthropogenic noise now reaches an unprecedented proportion of terrestrial landscapes, emanating from urban centers, aircraft, transportation networks, motorized recreation, and natural resource extraction (Barber et al. 2010). To our knowledge, this is the first study to investigate the spatial extent of chronic anthropogenic noise exposure from natural resource extraction and to link this exposure to ecological patterns that change in response to noise. The distances at which noise from a single compressor may impact birds in our study system are comparable to those reported by previous studies. For example, Bayne et al. (2008) reported that noise could affect bird communities up to 700 m from compressor stations in boreal forests of Alberta, Canada.

Our results suggest that the impact from a single compressor without noise-reducing walls may be at least 700 m, and much farther for a compressor station lacking noise-reducing walls. Under 2005 conditions, compressor noise reached over 80% of the study area, but the use of noise-reducing walls around existing compressors could lessen the spatial extent impacted by over 70%.

Despite the predicted effectiveness of noise-reducing walls at decreasing the area exposed to compressor noise, our results for broad-scale estimates for gray flycatcher and western scrub-jay occupancy would increase by only 5% and flycatcher nest success would be reduced by 8%. These apparently small changes occur because amplitudes within 5 dB(C) of baseline levels dominate the landscape under current management practices. Taken individually, these small improvements in occupancy may appear trivial compared to the relatively high costs associated with reducing noise amplitudes (see Bayne et al. 2008 for estimated costs of reducing compressor noise by 4 dB). However, it is critical to stress that reduced habitat use in response to noise is not restricted to the two species under consideration here, but that over one dozen species appear to be noise sensitive in our study area (Francis et al. 2009). Even though the analysis of flycatcher nest success was conducted independently of scrub-jay occupancy, it must be noted that jays depredate nests of many avian species; therefore, the increased nest predation risk associated with higher jay occupancies will be spread over dozens of bird species, many of which will also experience increased occupancy with decreased noise. Moreover, occupancy and nest success are only two ecological

patterns that may be influenced by noise exposure and many additional processes may change in response to noise (see below).

Ecological changes from noise exposure

Increases in nest success with increased noise amplitudes is not unique to flycatchers in our study area; similar patterns were observed for spotted towhees (*Pipilo maculatus*), chipping sparrows (*Spizella passerina*), and the pooled breeding bird community (Francis et al. 2009). Though we show how flycatchers may have increased rates of nest success throughout large areas throughout RCHMA due to the negative effect of noise on the scrub-jay, a major nest predator in the area, this pattern may not exist in other landscapes exposed to noise where different common nest predators may fail to respond to noise, or even respond positively.

Though birds nesting in areas exposed to compressor noise may benefit from decreased predation risk, which results in higher nest success, this single measure of reproductive success does not fully capture the full range of trade-offs that may occur for nesting birds exposed to noise. For example, great tit (*Parus major*) clutch size and the subsequent number of hatchlings and fledglings declines with increased noise exposure (W. Halfwerk, pers. comm.). Additionally, males may experience decreased pairing success relative to those in quiet areas. In Alberta, Canada, territory-holding male ovenbirds (*Seiurus aurocapilla*) were 17% less likely to successfully pair with a female in habitat adjacent to compressor stations relative to males holding territories in habitat adjacent to quiet well pads (Habib et al. 2007). A similar pattern was observed

for reed buntings (*Emberiza schoeniclus*) in Zurich, Switzerland (Gross et al. 2010). The exact mechanisms responsible for the reduced pairing success are unknown but may be due to females' decreased ability to detect and discriminate signals masked by noise, or, alternatively, the pattern may be an epiphenomenon of intraspecific competition. For instance, a greater proportion of territory-holding male ovenbirds in noisy areas were young and inexperienced relative to those in quiet areas (Habib et al. 2007). Because older, experienced males often acquire better territories (Holmes et al. 1996) and have higher pairing rates (Saether 1990; Bayne & Hobson 2001), younger territory-holding males in noisy habitat may be perceived as low quality mates relative to those in quiet areas. Studies determining whether reduced pairing success in noisy areas is typical across species and identifying the precise mechanisms responsible for this reduction are urgently needed.

That breeding birds may potentially benefit from noise in one sense, such as through reduced predation risk or a competitive release due to decreased densities of species less tolerant of noise (Francis et al. 2009; Slabbekoorn & Halfwerk 2009), but also suffer from detrimental effects, such as reduced pairing success or clutch size, limits our ability to quantify the net impact of noise on populations and communities. In terms of avian reproductive success, the way in which each breeding variable (e.g., breeding habitat occupancy, pairing success, clutch size, nest predation) responds to changes in noise amplitude and frequency will probably differ. For example, territory occupancy may have a near linear response to amplitude, pairing success may be described by a threshold response, and other stages may be described by different

linear and nonlinear functions. Unfortunately, our ability to understand how incremental changes to noise conditions influence these responses is restricted by the common use of study designs representing two extreme points on what is actually a continuous gradient of noise exposure (i.e., quiet vs. noisy habitat; Habib et al. 2007; Nemeth & Brumm 2009; Gross et al. 2010). Studies evaluating how processes respond to incremental changes to noise conditions are needed to determine how effects interact to influence population recruitment and long-term stability in landscapes exposed to noise. Yet, finding locations that permit the isolation of noise from other confounding stimuli to examine noise along amplitude and/or frequency gradients will be challenging, but critical to efforts scaling up population and community responses to noise to a broad-scale.

Another gap in our current understanding is how noise may influence animal movements. On fine spatial scales, con- and heterospecific acoustic signals are critical for spatial perception that may guide individuals to mating partners and prey items, or repel them from competitors and predators (Slabbekoorn & Bouton 2008). On broad spatial-scales, the use of acoustic cues for movements within a landscape ("soundscape orientation") may guide movements at great distances. For example, tropical coral larvae are attracted to acoustic cues to locate reef substrate for settlement and anthropogenic noise may disrupt larvae ability to use sound for orientation (Vermeij et al. 2010). Similar problems are likely to exist in terrestrial environments; because relatively small increases in noise amplitude may severely reduce an individual's listening area. Where soundscapes are dominated by anthropogenic noise, it is likely

that noise may present similar problems in terms of connectivity as do physically altered habitat structures and the spatial arrangement of the soundscape becomes important. Among the management scenarios we considered, adding walls around individual compressors or around central compression stations would greatly increase natural soundscape connectivity.

Extent of noise in RCHMA & the San Juan Basin and noise management

RCHMA has 400 km^2 with federally owned mineral rights (BLM 2003). Extrapolating from our analyses, 338 km^2 of RCHMA is exposed to elevated noise amplitudes due to compressors, and 244.4 km^2 have a listening area reduced by one-half or more. These estimates are most certainly low because they do not include noise amplitudes from traffic along the dendritic network of access roads, existing compressor stations along major pipelines, or drilling activities from the 600 new wells drilled each year in BLM managed land in NW New Mexico (Engler et al. 2001; BLM 2003).

In 2003, BLM anticipated an increase of nearly 10,000 new wells throughout the 5,666 km^2 of federally administered lands within the New Mexico portion of the San Juan Basin (BLM 2003), and half of the new wells are expected to have wellhead compression (Engler et al. 2001). This expansion in energy development is well underway and corresponds to considerable habitat loss and fragmentation for new well pads, pipelines and access roads. Compounding these changes to natural habitat with increased noise exposure from more compressors will likely only intensify the problems that arise due to these other anthropogenic forces. It is also important to recognize that

the San Juan Basin is not unique in this expected increase in energy extraction activities. Other landscapes throughout the United States and the world are slated for increases in gas extraction, such as the Marcellus Shale in New York, Pennsylvania and other eastern states (Kargbo et al. 2010) and the Barnett Shale in Texas (Bowker 2007). The anthropogenic component of soundscapes in these regions will almost certainly grow without management efforts.

For heavily developed landscapes with wellhead compression, use of noise-reducing walls may provide a good option to restore the natural soundscape and bring those ecological processes that had changed in response to noise back towards baseline levels. In landscapes at early stages of energy extraction development, central compression with noise-reducing walls may be a better option, especially if noise amplitudes are reduced by more than 10 dB(C), as we assumed in our model. In all cases, it is clear that without noise-reducing walls, the industry's soundscape footprint will be much larger and companies and land managers should work together to minimize the spatial distribution of this industry's impact on natural communities and maintain some semblance of the natural soundscape.

CHAPTER VII

CONCLUSION

In this dissertation I have explored the effects of noise exposure on avian communities. I found empirical evidence that noise, in the absence of other variables that often co-vary with noise, can strongly affect bird communities and that masking of vocal communication may be a primary mechanism precipitating large, community-level changes. It follows that when placed in the current global context, where few landscapes are untouched by anthropogenic noise, my findings suggest that noise may represent a severe threat to biodiversity.

That noise negatively influences birds is not a completely new result, but ecologists have focused primarily on (1) patterns of bird habitat use without adequately separating noise from other factors that could also explain changes in distributions (e.g., Kuitunen et al. 1998; Brotons & Herrando 2001; Forman et al. 2002; Peris & Pescador 2004; Palomino & Carrascal 2007; Delgado García 2008) or (2) signaling strategies employed by urban birds, without knowing whether such signal modifications in response to noise have associated fitness costs or whether signal modification is responsible for a species' ability to inhabit noisy urban areas (e.g., Slabbekoorn & Peet 2003; Brumm 2004; Wood & Yezerinac 2006; Fuller et al. 2007; Nemeth & Brumm 2009). In one sense it is somewhat surprising that researchers have not made attempts to bridge these two foci in attempt to link changes in bird distributions with species-

specific signaling properties and signaling flexibility, yet the high-dimensional nature of human disturbance has proven to be difficult to disentangle in most habitats, making bird sensitivities to noise difficult if not impossible to measure.

The patterns of decreased species richness and noise avoidance by numerous species presented in Chapter II provided the best evidence to date that noise can be detrimental to birds and confirms evidence for the many studies that had suggested that this was the case. However, Chapter II also provided evidence that some species, albeit a minority, appear to preferentially settle in noisy habitat over quiet habitat, despite no difference in over one dozen major habitat features. Additionally, nest success was higher in noisy areas and with increased noise exposure, as shown for real nests in Chapter II and with artificial nests in Chapter III. This pattern was opposite of long-standing concerns for noise-dependent reductions in nesting success (Warren et al. 2006; Slabbekoorn & Ripmeester 2008; Brumm 2010), and when placed in context of reduced predation risk, the preferential settlement in noisy habitat by some species begins to make sense.

Of course, settlement in noisy habitat over quiet habitat to benefit from reduced predation risk is only possible for species that can effectively communicate through, over, or around noise interference. Chapter IV linked responses to noise to vocal frequency, providing strong support for the acoustic masking hypothesis with troubling implications: those species most likely to persist in noisy habitats are smaller species with high-frequency vocalizations, but larger species with low-frequency signals may be functionally silenced and extirpated from otherwise suitable areas.

Chapter V, however, provided a more encouraging view: not all species are defenseless against masking effects of noise, as illustrated by the ash-throated flycatcher's persistence in noisy areas coupled with an increase in song frequency with increased noise exposure. Indeed, there are several behavioral mechanisms that may aid communication in noise, but, as also presented in Chapter V with the results pertaining to the gray flycatcher, not all species appear equipped with behavioral flexibility to overcome masking effects and these species may be forced to abandon noisy habitat. Moreover, whether the behavioral mechanisms employed by birds to overcome masking effects permits individuals to survive and reproduce under noisy conditions remains unknown, as little data on the costs and benefits associated with these mechanisms are available (Slabbekoorn & Ripmeester 2008). In one striking example, reed bunting males defending territories in noisy habitat use short-term frequency adjustments in response to noise exposure, but over 40% remained unpaired compared to only 8% of unpaired males in quiet locations (Gross et al. 2010). In other words, adjustments to be heard by the individual may have individual and population-level costs and pairing success is only one of many potential consequences of signal adjustments, as discussed in detail in Chapter VI. Thus, translating these individual-level behavioral responses to noisy conditions to population-level trends is far from straightforward, but will be a necessary component of future research understanding the cumulative consequences of noise exposure to local populations.

With so many potential consequences of noise exposure on species distributions and ecological processes, noise mitigation in and around human-altered habitat is

critical. In Chapter VI I showed that efforts to mitigate compressor noise in RCHMA can be effective; greatly reducing the anthropogenic noise “footprint” and maintaining patterns of habitat use and nest predation near “normal” (i.e., without any noise exposure). Technologies and methods to reduce noise propagation are readily available for industrial settings, as well as along roadways. Planners and managers could use noise barriers, depressed roadways, porous road surfaces, specific tire treads and even a “noise tax” to reduce noise exposure (Maekawa 1977; Sandberg 1991). Implementing these noise-mitigation efforts will be costly, especially retroactively, but these measures could greatly reduce one feature of the myriad of human activities that impact natural communities on a global scale. It is also worth noting that humans will also benefit from noise reduction measures implemented for wildlife.

In the future I will focus on two current gaps in our understanding of the effects of noise on natural communities: (i) signaling strategies to cope with noise (or lack of such strategies) and (ii) the cascading consequences of noise-dependent changes in species distributions on community function. First, there is a need to bridge the gap between evidence for flexible noise-dependent signaling that allow some species to persist in noisy areas and evidence for limited signal flexibility and avoidance of noisy habitat among other species (Chapters IV & V). A theoretical framework that places responses into a phylogenetic context is needed and will serve as a guide for clear predictions regarding how and why species adjust or fail to adjust signals. I will develop a framework based on the idea that there are intrinsic characteristics that differ among taxa that restrict signal flexibility in response to noise interference. The type and degree

of flexibility depends on phylogenetic history, current vocal function, and the nature of the interference noise. Mapping vocal parameters (e.g., frequency, temporal, amplitude features) onto phylogenies will help reveal the degree to which acoustic signals are phylogenetically conserved within and among avian taxa and will be immediately relevant to understanding the role of acoustics in structuring bird communities and for evaluating species sensitivities to noise pollution.

With respect to community-level changes in response to noise, much research to date has focused on presence/absence or changes in abundance of individual species (e.g., Forman et al. 2002; Bayne et al. 2008), presumably in direct response to noise exposure. However, my research has shown that noise-dependent changes in species' abundances can affect demographic patterns for other species, such as nest success, and perhaps patterns of species abundance via settlement choices. In other words, some changes may be caused indirectly and such patterns would be impossible to gauge without a community-level focus. It should be expected then that altered avian community assemblages, whether directly or indirectly due to noise, will have consequences on non-avian community members, especially those species that depend on birds for ecological services (Sekercioglu 2006). In RCHMA, noise-dependent distributions of western scrub-jays and black-chinned hummingbirds may have consequences for plant communities that depend on these species. Yet because these species have opposite responses to noise in terms of their habitat use, the corresponding effects on plant species may be negative or positive. For example, noise-dependent decreases in scrub-jay abundance may negatively influence piñon pine

seedling establishment, due to piñon pine's reliance on scrub-jays and other corvids as mobile links for seed dispersal (Vander Wall & Balda 1981; Chambers et al. 1999). Conversely, black-chinned hummingbird's preferential use of noisy habitat could benefit hummingbird-pollinated flowers. These are but two examples of studies that may focus on the botanical implications of noise exposure, but begin to address a broader question: How does noise exposure translate into future assemblages of both plant and animal communities?

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